

ANIMAL NUTRITION

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Animal Nutrition

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CONTENTS

	PAGE
FOREWORD	VII
PREFACE	IX

CHAPTER		
1	The Animal and its Food	1
2	Carbohydrates	6 ✓
3	Lipids	21
4	Proteins	34
5	<i>Vitamins</i>	48
6	Minerals	75
7	Enzymes	97
8	Digestion	104
9	Metabolism	123
10	The Evaluation of Foods (A) Digestibility	144
11	The Evaluation of Foods (B) The Energy Content of Foods and the Partition of Food Energy within the Animal	156
12	The Evaluation of Foods (C) Systems of Expressing the Energy Value of Foods	181
13	The Evaluation of Foods (D) Protein	200
14	Feeding Standards for Maintenance and Growth	214
15	Feeding Standards for Reproduction and Lactation	252
16	Grass and Forage Crops	295
17	Silage	306
18	Hay, Artificially Dried Grass, Straws, and Chaff	314
19	<i>Roots and Tubers</i>	324
20	Cereal Grains and Cereal By-products	331
21	Protein Concentrates	343
22	Growth-stimulating Substances	358

APPENDIX:

	Note on the use of the Tables	368
TABLE		
1	Nutritive Value of Foods for Ruminants	370
2	Nutritive Value of Foods for Pigs	374
3	Nutritive Value of Foods for Poultry	376

TABLE

4	Amino Acid Composition of Foods	378
5	Vitamin Content of Foods	380
6	Mineral Content of Foods	381
7	Feeding Standards for Dairy Cattle	384
8	Feeding Standards for Beef Cattle	385
9	Feeding Standards for Sheep	386
10	Feeding Standards for Pigs	387
11	Feeding Standards for Poultry	388

INDEX

391

FOREWORD

In the economics of animal production the cost of foodstuffs is an item of the greatest importance, and the keynote to efficiency is the proper utilisation of the nutrients they contain. To ensure this it is essential to understand clearly the principles of animal nutrition. Modern advances in biochemistry and physiology have added much to our knowledge of the plant that is the source of nutrients, and also of the animal that consumes these nutrients.

This book is the outcome of the experience of three members of the staff of the Edinburgh School of Agriculture in the teaching of animal nutrition and in dealing with the problems of feeding livestock that arise in the agricultural industry.

The first section covers the constituents of the foodstuffs and shows the great increase in our knowledge of these that has been made possible by modern techniques. The rough grouping of the constituents that sufficed for the earlier workers in animal nutrition has given way to a detailed study of the various chemical entities that make up each group and has led to a better understanding of its function in the nutrition of the animal.

The digestion and metabolism of the constituents follow, and here again it is evident that much more is known of these processes. This information has allowed of a fuller evaluation of the foodstuffs, and with it an increased appreciation of their true value and of the use made of them by the vital processes of the animal.

With this background it is possible to formulate feeding standards. To this end the Agricultural Research Council of Great Britain has recently set up working parties, and their recommendations will bring up to date the accumulated knowledge and should be of immense value.

The final section gives an account of the various groups of foodstuffs available and their characteristics. It is, however, not possible within the compass of such a book to deal with them as exhaustively as has been the case in earlier books on animal nutrition, nor in point of fact is it necessary to do so.

Whilst this book is designed in the first instance for the student aiming at the degree in agriculture it should prove of great value to all students, and will be of value also to the farmer, even though he may not require all the detail essential to a proper understanding of animal nutrition.

S. J. WATSON

PREFACE

This book is intended to be an introduction to the study of the nutrition of farm animals. Although it is written primarily for agricultural students, it is hoped that it will be useful for students of veterinary science and allied subjects, and also for agricultural advisers and progressive farmers.

In writing this textbook we have emphasised the biochemical aspects of nutrition; this has been done intentionally, since a proper understanding of the subject is impossible without a knowledge of biochemical processes. We have dealt with the theoretical basis of nutrition rather than with different practical feeding systems, since we feel that the latter are best included in animal husbandry textbooks.

Although the reader does not require any previous knowledge of biochemistry, it is assumed that he will have received some basic training in organic chemistry and the biological sciences.

We have not attempted to give detailed lists of references to original papers; students wishing to obtain more information are referred to the textbooks and review articles listed at the end of each chapter and to the periodical *Nutrition Abstracts and Reviews*.

The authors are indebted to many people for advice and help. We would particularly like to thank Professor S. J. Watson for writing the Foreword, and for giving helpful criticisms and suggestions during the planning of this book. We are grateful to Dr W. Bolton for reading the whole manuscript and giving his comments as well as kindly providing Plates 1 to 5, and to Dr J. A. Watt for veterinary advice and for providing Plate 6. We are indebted to Drs D. G. Armstrong, D. J. Bell, W. A. Dewar, A. W. MacGregor, H. T. Maepherson, T. B. Miller and D. Purves for reading and commenting on certain chapters and to Professor I. A. M. Lucas and Mr J. W. Dent for advice on construction of some of the tables. We also thank Dr K. L. Blaxter for reading part of the manuscript and for providing some data which were at the time unpublished. We are grateful to Mr G. Finnie for his skilled assistance with some of the figures. We would also like to record our thanks to our wives for their invaluable help in typing, proof-reading and general comment. Finally we would like to thank the publishers for the trouble they have taken and the help they have given.

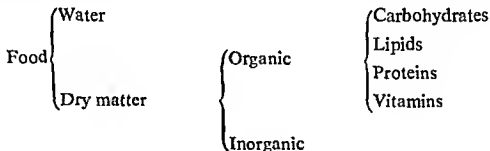
THE ANIMAL AND ITS FOOD

Food is the material which after ingestion by animals is capable of being digested, absorbed and utilised. In a more general sense we use the term 'food' to describe edible material. Grass and hay, for example, are described as foods, but not all their components are digestible. Where the term 'food' is used in the general sense, as in this book, then those components capable of being utilised by animals are described as *nutrients*.

COMPONENTS OF FOODS AND ANIMALS

The major part of the diet of farm animals is made up of plant material; foods of animal origin such as fish meal, meat meal and milk products are provided in limited amounts only—mainly for pigs and poultry.

Plants and animals contain similar types of chemical substances, and we can group many of these into classes according to constitution, properties or function. The main components of foods (and animals) are:



Water

The water content of the animal body varies with age. The newborn animal contains from 75 to 80 per cent. water, but this falls to about 50 per cent. in the mature fat animal. It is vital to the life of the organism that the water level in the body be maintained—an animal will die more rapidly if deprived of water than if deprived of food. Water functions in the body as a solvent in which nutrients are transported about the body and in which waste products are excreted. Many of the chemical reactions brought about by enzymes take place

in solution and involve hydrolysis. Because of the high specific heat of water, large changes in heat production can take place within the animal with very little alteration in body temperature. Water also has a high latent heat of evaporation, and its evaporation from the lungs and skin gives it a further role in the regulation of body temperature.

The animal obtains its water from three sources: drinking water, water present in its food and metabolic water, this last being formed during metabolism by the oxidation of hydrogen containing organic nutrients. The water content in food is very variable and, as the figures in Table 1.1 indicate, can range from 6 per cent in concentrates to over 90 per cent in some root crops. The water content of growing plants is related to the stage of growth, younger plants containing more water than older plants. In temperate climates drinking water is not usually a problem and animals are provided with a continuous supply. There is no evidence that under normal conditions an excess of drinking water is harmful, and animals normally drink what they require.

Dry Matter

The dry matter of foods is conveniently divided into organic and inorganic material, although in living organisms there is no such sharp distinction. Many organic compounds contain mineral elements as structural components. All proteins, for example, contain sulphur, while many of the lipids and carbohydrates in plants and animals contain phosphorus.

It can be seen from Table 1.1 that the main component of the dry matter of pasture grass is carbohydrate, and this is true of all plants and many seeds—the oilseeds, such as groundnuts, being exceptional in containing large amounts of protein and of lipid material in the form of fat or oil. In contrast the carbohydrate content of the animal body is very low. One of the main reasons for the difference in carbohydrate content between plants and animals is that, whereas the cell walls of plants consist of carbohydrate material, mainly cellulose, the walls of animal cells are composed almost entirely of protein. Furthermore, plants store energy largely in the form of carbohydrates such as starch and fructosans, whereas an animal's main energy store is in the form of fat.

Fat is the most important lipid present in both plants and animals. The fat content of the animal body is variable and is related to age, the older animal containing a much greater percentage of fat than the young animal. The lipid content of living plants is relatively low, that of pasture grass dry matter, for example, being 4 to 5 per cent.

In both plants and animals, proteins are the major nitrogen-containing compounds. In plants, where most of the protein is present as enzymes, the percentage is high in the young growing plant and falls as the plant matures. In animals, muscle, tissues, skin, hair, feathers, wool and nails are composed of protein.

Vitamins are present in plants and animals in minute amounts, and many of them are important as components of enzyme systems. When considering vitamins, the essential difference between plants and animals is that, whereas the former can synthesise all the vitamins they require for metabolism, the animal cannot, or has very limited powers of synthesis, and is dependent upon an external supply.

TABLE 1.1. Percentage Composition of some Plant and Animal Products

	<i>Water</i>	<i>Carbohydrate</i>	<i>Fat</i>	<i>Protein</i>	<i>Ash</i>
Turnips ✓	91	7 1	0 2	1 0	0 7
Pasture grass ✓ (young leafy)	80	10 0	1 0	3 2	2 4
Wheat grain ✓	13	71 2	1 9	12 2	1·7
Groundnuts ✓	6	20 1	44 9	26 8	2 2
Dairy cow ✓	57	0 2	20 6	17 2	5 0
Blood ✓	82	0 1	0 6	16 4	0 7
Liver ✓	74	1 3	6 5	16 8	1·4
Muscle .	72	0 6	4 3	21·4	1 5
Milk (cow's)	87 6	4 7	3 6	3 3	0 8

The inorganic matter contains all those elements present in plants and animals other than carbon, hydrogen, oxygen and nitrogen. Calcium and phosphorus are the major components of the ash of animals, whereas potassium and silicon are the main inorganic elements in plants.

ANALYSIS OF FOODS

Modern methods of analysis, including the use of chromatographic and spectrochemical techniques, make it possible to determine individual carbohydrates, proteins, fats, vitamins and mineral elements. Detailed information of this kind is, however, tedious to obtain unless expensive automatic analytical equipment is available. Much of the existing information we have about the composition of foods is based on a method described as the *proximate analysis of foods*, devised about 100 years ago by two German scientists, Henneberg and Stohmann.

Proximate Analysis of Foods

This system of analysis divides the food into six fractions, as shown in Table 1.2.

The moisture content is determined as the percentage loss in weight which results from drying a known weight of food at 100° C to constant weight. This method is satisfactory for most foods, but with a few, such as silage, significant losses of volatile material may take place.

The ash content is determined by ignition of a known weight of the food at 500° C until all carbon has been removed. The residue is the ash and is taken to represent the inorganic constituents of the food. The ash may, however, contain material of organic origin such as sulphur and phosphorus from proteins, and some loss of volatile material in the form of sodium, chloride, potassium, phosphorus and sulphur will take place during ignition. The ash content is thus not truly representative of the inorganic material in the food either qualitatively or quantitatively.

TABLE 12 Components of Different Fractions in the Proximate Analysis of Foods

<i>Fraction</i>	<i>Components</i>
Moisture	Water (and volatile acids and bases if present)
Ash	Essential elements { Major Ca, K, Mg, Na, S, P, Cl Trace Fe, Mn, Cu, Co, I, Zn, Mo, Se Probably essential elements F, Br, Ba, Sr Non-essential elements Si, Cr, Ni, Ti, Al, V, B, Pb, Sn
Crude protein	Proteins, amino acids, amines, nitrates, nitrogenous glycosides, glycolipids, B vitamins
Ether extract	Fats, oils, waxes, organic acids, pigments, sterols, vitamins A, D, E, K
Crude fibre	Cellulose, hemicelluloses, lignin
Nitrogen free extractives	Cellulose, hemicelluloses, lignin, sugars, fructosans, starch, pectins, <u>organica</u> acids, <u>resins</u> , <u>tannins</u> , pigments, water soluble vitamins

The crude protein content is calculated from the nitrogen content of the food, determined by a modification of the Kjeldahl sulphuric acid digestion technique. In this method the food is digested with sulphuric acid, which converts to ammonia all nitrogen present except that in the form of nitrate and nitrite. This ammonia is liberated by adding sodium hydroxide to the digest, distilled off and collected in standard acid, the quantity so collected being determined by titration. It is assumed that the nitrogen is derived from protein containing 16 per cent nitrogen, and by multiplying the nitrogen figure by 100/16 or 6.25 an approximate protein value is obtained. This is not 'true protein' since the method determines nitrogen from sources other than protein, and the fraction is therefore designated crude protein.

The ether extract fraction is determined by subjecting the food to a continuous extraction with petroleum ether for a defined period. The residue, after evaporation of the solvent so obtained, is the ether extract. As well as true fat it contains waxes, organic acids, alcohols and pigments, designation of the fraction as 'oil' or 'fat' is therefore incorrect.

The carbohydrate of the food is contained in two fractions, the crude fibre and the nitrogen-free extractives. The former is determined by subjecting the residual food from ether extraction to successive treatments with boiling acid and alkali of defined concentration, the organic residue is the crude fibre. When the sum of the percentages of moisture, ash, crude protein, ether extract and crude fibre is subtracted from 100, the difference is designated the nitrogen-free extractives (NFE). The crude fibre fraction contains cellulose, lignin and hemicelluloses, but not necessarily all of these materials present in the food: a variable proportion of them is contained in the nitrogen-free extractives, depending upon the species and stage of growth of the plant material. The complexity of the nitrogen free extractives fraction is well illustrated by the constituents shown in Table 1.2. The crude fibre was intended originally to provide a measure of the indigestible part of the food, but quite a large part of it may in fact be digested by ruminant animals. Despite this the figure is valuable because of the correlation existing between it and the digestibility of the food.

Although inadequate as a measure of the chemical composition, the proximate analysis provides useful information on the nutritive value of foods in general and it is still retained as a routine method of analysis. Most laboratories, however, supplement the data obtained from proximate analysis with more detailed analyses carried out by modern techniques.

FURTHER READING

Fertiliser and Feeding Stuffs Regulations, 1960 H M S O, London
U S D A Year Book 1955 Water U S Government Printing Office, Washington,
D C, U S A

CARBOHYDRATES

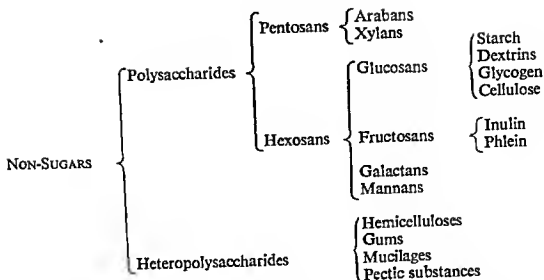
The name carbohydrate is derived from the French *hydrate de carbone* and was originally applied to neutral chemical compounds containing the elements carbon, hydrogen and oxygen with the last two elements in the same proportion as in water. This definition still applies to the majority of the group, although the term now includes a number of sugar derivatives and their polymers.

Classification of Carbohydrates

The carbohydrates are usually divided into two major groups, the sugars and the non-sugars (see Table 2.1). The simplest sugars are monosaccharides, which are divided into the sub-groups pentoses ($C_5H_{10}O_5$) and hexoses ($C_6H_{12}O_6$) depending upon the number of carbon atoms present in the molecule. Monosaccharides may be linked together, with the elimination of one molecule of water at each linkage, to produce di-, tri- or polysaccharides containing respectively 2, 3 or large numbers of monosaccharide units or residues.

TABLE 2.1 Classification of Carbohydrates

SUGARS	Monosaccharides	Pentoses $C_5H_{10}O_5$	{ Arabinose Xylose Ribose
		Hexoses $C_6H_{12}O_6$	{ Glucose Galactose Mannose Fructose
	Disaccharides $C_{12}H_{22}O_{11}$		{ Sucrose Lactose Maltose Cellobiose Trehalose
	Trisaccharides $C_{18}H_{32}O_{16}$		Raffinose
	Tetrasaccharides $C_{24}H_{42}O_{21}$		Stachyose



The term sugar is generally restricted to those carbohydrates containing less than ten monosaccharide residues, while the name oligosaccharides (*oligo*-, few) is frequently used to include all sugars other than monosaccharides.

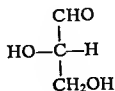
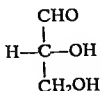
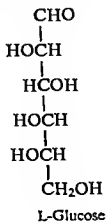
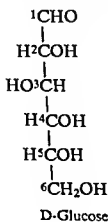
Polysaccharides are classified according to the kind of sugar which they produce on hydrolysis. For example glucosans are condensation polymers of glucose, fructosans of fructose and xylans of xylose. Hydrolysis of these polymers to their constituent sugars can be brought about by the action of either specific enzymes or acids.

Heteropolysaccharides are mixed polysaccharides which on hydrolysis yield mixtures of monosaccharides and derived products.

MONOSACCHARIDES

Structure

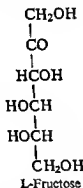
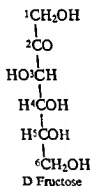
The formula for glucose may be represented in the form of a straight chain. Two stereoisomeric forms are possible:



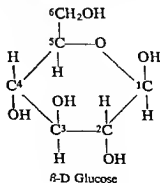
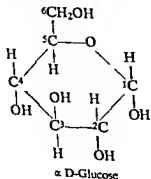
The forms are designated D and L-glucose, depending upon the direction of the hydroxyl group on the penultimate carbon atom (C_5). For this nomenclature the D and L-forms of the triose glycerose are used as reference compounds, as shown in the above formulae

It can be seen that the formulae contain an aldehyde (CHO) group, and sugars containing this group are classed as aldoses. Because of the presence of 4 asymmetric carbon atoms in aldohexoses, there are 16 possible stereoisomeric forms 8 of these being D sugars and the other 8 mirror images of these or L-forms. Only a few of these occur naturally, in addition to D glucose the important ones are D galactose and D mannose

The hexose straight chain formula may contain a ketone group (CO) instead of an aldehyde group. Sugars containing a ketone group are classed as ketoses. Eight stereoisomers are possible, 4 D forms and 4 L-forms. The only naturally occurring ketohexose is D fructose



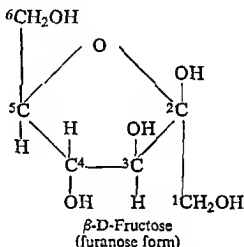
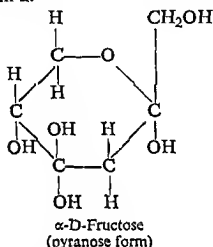
Certain facts suggest that sugars can exist in a ring or cyclic form. In the case of D glucose the structure is in the form of a pyranose ring similar to pyran. Two forms of D glucose occur, known as α and β glucose depending upon the configuration of carbon atom 1. In



the ring form carbon atom 1 becomes asymmetric, which doubles the number of isomeric sugars in any one group. A pair of stereoisomers related to each other as are α - and β -D-glucose are said to be anomers, and carbon atom 1 is termed the anomeric carbon atom.

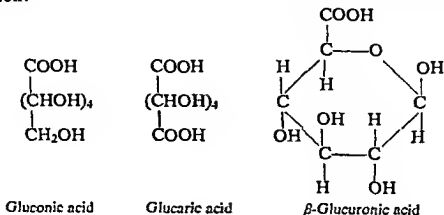
Derivatives of both α - and β -D-glucose occur. Starch and glycogen are both polymers of the α -form, while cellulose is a polymer of β -glucose.

As with glucose, fructose normally exists as a ring, which may be 6-membered but is more commonly a 5-membered or furanose ring similar to furan. In the furanose form, the anomeric carbon is carbon atom 2.



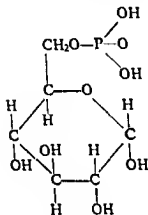
Properties of the Monosaccharides

Because of the presence of an active aldehyde or ketone grouping, the monosaccharides act as reducing substances. They can be oxidised to produce a number of acids. In the case of glucose, partial oxidation of the open-chain compound results in the formation of gluconic acid. Further oxidation produces glucaric acid (saccharic acid). When glucose exists in the cyclic form, then glucuronic acid is produced on oxidation:

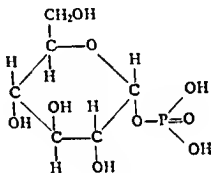


The most important sugar acids are the uronic acids, especially glucuronic and galacturonic acids, which are components of the heteropolysaccharides.

An important property of the monosaccharides is their reaction with phosphoric acid. A number of sugar phosphates occur naturally in both plants and animals, two important compounds being glucose-6-phosphate and glucose-1-phosphate:



Glucose-6-phosphate



Glucose-1 phosphate

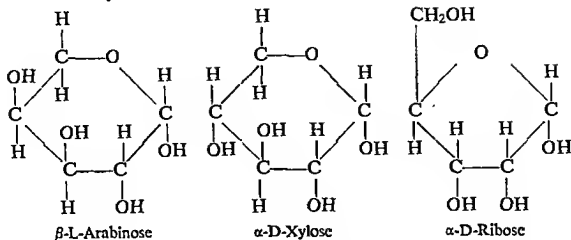
Hexose phosphates play a very important role in cell metabolism

Pentoses

Pentoses have the general formula $C_5H_{10}O_5$. The most important members of this group of simple sugars are L-arabinose, D-xylose and D-ribose. These sugars rarely occur free in nature, except as breakdown products during fermentation. Arabinose and xylose residues occur in pentosans, which are constituents of hemicelluloses. Both these sugars are produced in considerable quantity when herbage is hydrolysed with normal sulphuric acid. Arabinose also occurs in gum-arabic and other gums.

Ribose is present in all living cells as a constituent of ribonucleic acid (RNA), and is also a constituent of several vitamins and coenzymes. Pentoses can exist in the open-chain or the ring form. They show similar reducing properties to the hexoses, but are not fermented by yeast. The three pentose sugars described above are

dextrorotatory:



Hexoses

Glucose and fructose are the most important naturally occurring hexose sugars, while mannose and galactose occur in plants in a polymerised form as mannans and galactans.

D-Glucose, grape sugar or dextrose exists in the free state as well as in combined form. The sugar occurs free in plants, fruits, honey, blood, lymph and cerebrospinal fluid, and is the sole or major component of many oligosaccharides, polysaccharides and glucosides. In the pure state, glucose is a white crystalline solid and like all sugars is soluble in water. It is dextro-rotatory and reacts as a typical aldohexose.

D-Fructose, fruit sugar or laevulose occurs free in green leaves, fruits and honey. It also occurs in the disaccharide sucrose and in fructosans. Green leafy crops usually contain appreciable amounts of this sugar both free and in polymerised form. The free sugar is a white crystalline solid and has a sweeter taste than sucrose. The exceptionally sweet taste of honey is due to this sugar. Fructose differs from the other hexoses in being laevo-rotatory.

D-Mannose does not occur free in nature but exists in polymerised form as mannan, and also as a component of glycoproteins. The free sugar is dextro-rotatory.

D-Galactose does not exist free in nature except as a breakdown product during fermentation. It is present as a constituent of the disaccharide lactose, which occurs in milk. Galactose also occurs as a component of the anthocyanin pigments, galactolipids, gums and mucilages. The sugar is dextro-rotatory.

Glycosides

If the hydrogen of the hydroxyl group attached to the anomeric carbon atom of glucose is replaced by esterification or by condensation

with an alcohol (including a sugar molecule) or a phenol, the derivative so produced is termed a glucoside. Similarly galactose forms galactosides, and fructose forms fructosides. The general term glycoside is used collectively to describe these derivatives, and the linkage effected through the anomeric carbon atom is described as a glycosidic bond.

Oligosaccharides, polysaccharides and heteropolysaccharides are all classed as glycosides, and these compounds yield sugars or sugar derivatives on hydrolysis. Certain naturally occurring glycosides contain non-sugar residues. For example the nucleosides contain a sugar combined with a heterocyclic nitrogenous base (see Chapter 4).

The cyanogenetic glycosides liberate hydrogen cyanide (HCN) on hydrolysis, and because of the toxic nature of this compound plants containing this type of glycoside are potentially dangerous to animals. The glycoside itself is not toxic and must be hydrolysed before poisoning occurs. However the glycoside is easily broken down to its components by means of an enzyme which is usually present in the plant.

An example of a cyanogenetic glycoside is linamarin (also called phaseolunatin), which occurs in linseed, Java beans and cassava. If wet mashies or gruels containing these foods are given to animals, it is advisable to boil them when mixing in order to inactivate any enzyme present. On hydrolysis linamarin yields glucose, acetone and hydrogen cyanide.

Examples of other cyanogenetic glycosides and their sources are shown in Table 2.2.

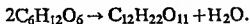
TABLE 2.2 Some Important Naturally Occurring Cyanogenetic Glycosides

Name	Source	Hydrolytic products in addition to glucose and hydrogen cyanide
Linamarin (phaseolunatin)	Linseed (<i>Linum usitatissimum</i>) Java beans (<i>Phaseolus lunatus</i>) Cassava (<i>Mamhot esculenta</i>)	Acetone
Vicianin	Seeds of wild vetch (<i>Vicia angustifolia</i>)	Arabinose, benzaldehyde
Amygdalin	Bitter almonds, kernels of peach, cherries, plums, apples and fruits of Rosaceae	Benzaldehyde
Dhurrin	Leaves of the great mullet (<i>Sorghum vulgare</i>)	p-hydroxy-benzaldehyde
Lotaustralin	Trefoil (<i>Lotus australis</i>) White clover (<i>Trifolium repens</i>)	Methylethyl ketone

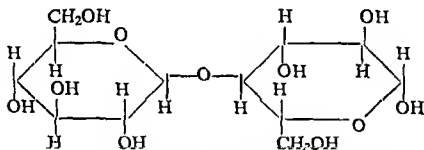
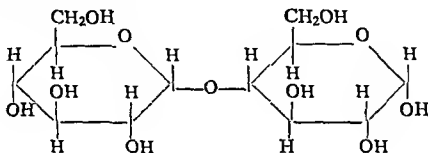
DISACCHARIDES

Structure

Disaccharides consist of two molecules of hexose sugars condensed together with the loss of one molecule of water:

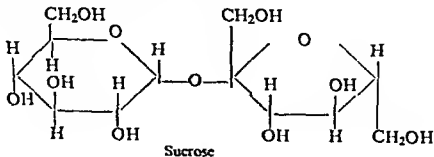


A large number of disaccharide compounds are possible, depending upon the hexoses present and the manner in which they are linked. The most important are sucrose, maltose, lactose, cellobiose and trehalose. Maltose and cellobiose both consist of two glucose residues linked in the 1,4 positions, but differ structurally, as can be seen from the following formulae:



Both maltose and cellobiose have one active reducing group and show reducing properties. Trehalose consists of two glucose residues linked in the 1,1 positions and is therefore non-reducing.

Sucrose consists of one molecule of glucose and one molecule of fructose joined together through their reducing groups, and therefore this disaccharide is also non-reducing:



Lactose consists of one molecule of glucose joined to one of galactose and has one active reducing group

Sucrose, cane sugar, beet sugar or saccharose is the familiar sugar of domestic use. It is widely distributed in nature and occurs in most plants. Sugar cane contains about 20 per cent of sucrose and sugar beet 15 to 20 per cent, it is also present in other roots such as mangolds and carrots, and occurs in many fruits. Sucrose is easily hydrolysed by the enzyme sucrase or by dilute acids. When sucrose is heated to a temperature of 160°C it forms barley sugar and at a temperature of 200°C it forms caramel. Sucrose is dextro-rotatory.

Lactose, or milk sugar, occurs only as a product of the mammary gland. Cows' milk contains 4.6 to 4.8 per cent. Lactose is not as soluble as sucrose and is less sweet, imparting only a faint sweet taste to milk. It is dextro-rotatory.

Lactose readily undergoes fermentation by a number of organisms, including *Streptococcus lactis*, the organism responsible for the souring of milk by converting the lactose into lactic acid ($\text{CH}_3\text{CHOHCOOH}$). If lactose is heated to 150°C it turns yellow, and at a temperature of 175°C the sugar is changed into a brown compound, lactocaramel. On hydrolysis lactose produces one molecule of glucose and one molecule of galactose.

Maltose, or malt sugar, is produced during the hydrolysis of starch and glycogen by dilute acids or enzymes. This sugar is produced from starch during the germination of barley by the action of the enzyme diastase. The barley after germination and drying is known as malt and is used in the manufacture of beer. Maltose is water soluble, but is not as sweet as sucrose. It is dextro-rotatory, and on hydrolysis yields two molecules of glucose.

Cellobiose does not exist naturally as a free sugar, but is the basic repeating unit of cellulose. Cellobiose can be hydrolysed to glucose, and its properties are similar to maltose although it is less soluble and less sweet.

Trehalose is a disaccharide present in fungi and seaweeds.

TRISACCHARIDES

Trisaccharides are formed by the union of three molecules of hexose sugars



Raffinose is the commonest member of the group occurring almost as widely in plants as sucrose. It exists in small amounts in sugar beet,

and accumulates in molasses during the commercial preparation of sucrose. Cotton seed contains about 8 per cent. of raffinose. On hydrolysis this sugar produces glucose, fructose and galactose. It is non-reducing.

TETRASACCHARIDES

Tetrasaccharides are produced by the union of four hexose residues:



Stachyose is an example of a tetrasaccharide, and has been isolated from about forty different plant species. It occurs in the seeds of leguminous plants and in the roots of the *Stachys* genus (Woundworts). It is a non-reducing sugar and hydrolyses to two molecules of galactose, one molecule of glucose and one of fructose.

POLYSACCHARIDES

These carbohydrates are very different from the sugars. The majority are of high molecular weight, being composed of large numbers of pentose or hexose residues. Polysaccharides do not possess a sweet taste, and do not give the various sugar reactions characteristic of the aldoses and ketoses. Many of them occur in plants either as reserve food materials such as starch or as structural materials such as cellulose.

The polysaccharide group is limited generally to the monosaccharide condensation polymers which contain ten or more monosaccharide residues. *The division is generally very distinct, since most naturally occurring oligosaccharides contain only two or three monosaccharide units, whereas the majority of the polysaccharides contain from a hundred to several thousand units.*

Pentosans

Arabans and xylans occur in combination with other materials in plants. The former produce arabinose on hydrolysis, while xylans produce xylose. Pentosans are important components of hemicelluloses and will be referred to in more detail under the section dealing with these heteropolysaccharides.

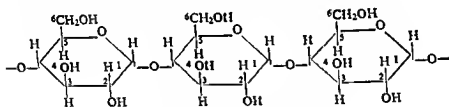
Hexosans

Starch is a glucosan (or glucan), and is present in many plants as a reserve carbohydrate. It is most abundant in seeds, which may contain up to 70 per cent., and in fruits, tubers and roots, which may contain 30

per cent Starch occurs naturally in the form of granules, whose size and shape vary in different plants. The granules are built up in concentric layers, and although glucosan is the main component of the granules they also contain minor constituents such as protein, fatty acids and phosphorus compounds which may influence their properties.

Starches differ in their chemical composition, and except in rare instances are mixtures of two structurally different polysaccharides termed amylose and amylopectin. The proportions of these present in natural starches depend upon the source, although the proportion found in most cereal grains and potatoes is 20 to 28 per cent amylose and 80 to 72 per cent amylopectin. The quantity of amylose can be estimated in starches by a characteristic reaction with iodine. Amylose produces a deep blue colour while amylopectin solutions produce a blue violet or purple colour.

A study of the two major fractions of starch has shown that amylose is composed of linear molecules in which the α -D glucose residues are linked between carbon atom 1 of one molecule and carbon atom 4



Part of amylose molecule showing 1,4 linkages

of the adjacent molecule. Amylopectin has a bush like structure containing primarily α 1,4 linkages, but the molecule also contains side-chains in which carbon atom 6 of certain glucose residues is linked with carbon atom 1 of the other glucose residues.

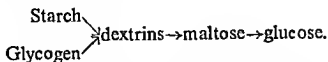
Starch granules are insoluble in cold water, but when a suspension in water is heated the granules swell and eventually the granule sacs rupture, and a gelatinous solution is formed.

Animals consume large quantities of starch in cereal grains, cereal by products and tubers. This carbohydrate lends its name to the feeding standard 'Starch Equivalent', which is used widely in the U.K. as an energy unit in the rationing of farm animals.

Glycogen is a term used to describe a group of highly branched polysaccharides isolated from animals or micro organisms. Glycogens occur in liver, muscle and other animal tissues. They are glucosans,

analogous to amylopectin in structure, and have been referred to as 'animal starches'. They form colloidal solutions which are dextro-rotatory. Glycogen is the main carbohydrate storage product in the animal body and plays an essential role in energy metabolism.

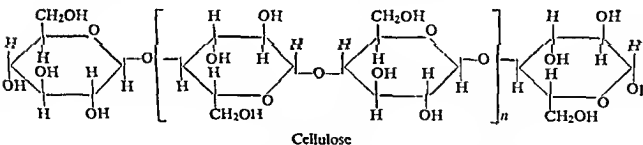
Dextrins are intermediate products of the hydrolysis of starch and glycogen:



Dextrins are soluble in water and produce gum-like solutions. The higher members of these transitional products produce a red colour with iodine, while the lower members do not give a colour. The presence of dextrins gives a characteristic flavour to bread crust, toast and partly charred cereal foods.

Cellulose is a glucosan and is the most abundant plant constituent, forming the fundamental structure of plant cell walls. The cell wall material contains other ingredients, and recent evidence suggests that there might be a chemical linkage between cellulose and hemicelluloses as well as between cellulose and lignin. Despite this close association cellulose does occur in a nearly pure form in cotton.

Pure cellulose is a polysaccharide of high molecular weight, in which the repeating unit is cellobiose. Here the β -glucose residues are 1,4 linked:



The value of n in this formula varies from about 100 to 4000, depending upon the source of the cellulose.

This polysaccharide is more resistant to chemical reagents than other glucosans, but it can be hydrolysed to glucose by cold strong acids. Certain enzymes also attack cellulose and produce cellobiose, which can be hydrolysed to glucose by cellobiase. These cellulase enzymes which attack cellulose occur in germinating seeds, fungi and bacteria, but are not secreted by animals. Microbial fermentation of cellulose occurs to some extent in the digestive tract of most animals, particularly in ruminants. The end-product of this fermentation is usually a

mixture of acids including acetic, propionic and butyric, as well as gases such as methane, carbon dioxide and, under some conditions, hydrogen

Fructosans (or fructans) occur as reserve material in the roots, stems, leaves and seeds of various plants, particularly in the Compositae and Gramineae. These polysaccharides are soluble in cold water and are of relatively low molecular weight. They can be broadly classified into two main groups according to their molecular structure: the inulin group and the phlein group. The former includes inulin, asparagosan and graminan, the latter phlean, levan and poan. Of these inulin has received more attention than the others, it appears to replace starch in the leaves and roots of the Compositae. Inulin produces on hydrolysis D fructose and a small quantity of glucose. This trace of glucose is frequently produced on hydrolysis of fructosans, indicating that many naturally occurring fructosans have a terminal sucrose unit in their structure. Phlein is present in the tubers of the grass *Phleum pratense* (Timothy). Many grasses contain appreciable quantities of fructosans, for example quantities ranging from 2 to 18 per cent in the dry matter of ryegrass have been reported.

Galactans and mannans are polysaccharides which occur in the cell walls of plants. A mannan is the main component of the cell walls of palm seeds, where it occurs as a food reserve and disappears during germination. A rich source of mannan is the endosperm of nuts from the South American tague tree, the hard endosperm of this nut is known as vegetable ivory. The seeds of many legumes, including clovers, trefoil and lucerne, contain galactans.

HETEROPOLYSACCHARIDES

Hemicelluloses are a group of compounds which accompany cellulose in the leafy and woody structures of plants, and in certain seeds. It is an ill-defined group whose members differ from cellulose in being hydrolysed by boiling with dilute acid, producing sugars and generally uronic acids. Sugars frequently produced on hydrolysis are xylose, glucose, galactose and arabinose, in many grasses xylose predominates.

The name hemicellulose is misleading and implies that the material is destined for conversion to cellulose. Although this was assumed originally to be the ultimate fate for hemicelluloses, it is now known that these heteropolysaccharides are not precursors of cellulose.

Modern methods of chromatographic analysis enable individual pentose and hexose determinations to be made on hydrolysed plant

extracts of hemicelluloses. Where this system of analysis has been adopted results are frequently expressed in amounts of xylan, araban galactan, etc.

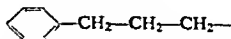
Gums are often produced from wounds in plants, although they may arise as natural exudations from bark and leaves. These exudates, which on drying in air thicken to a translucent glassy mass, are often composed of polysaccharides. Gums are very complex compounds which may be hydrolysed to monosaccharides and uronic acids. Gum-arabic (acacia gum) has long been a familiar substance; it is soluble in water and upon hydrolysis yields arabinose with small amounts of galactose, glucuronic acid and a sugar derivative, rhamnose.

Mucilages are found in certain plants and seeds, and like the gums are complex substances. Linseed mucilage is a well-known example of this type of compound, and produces arabinose, rhamnose, galactose and galacturonic acid on hydrolysis. Many algae yield mucilages which are soluble in hot water and form a gel on cooling. Agar is an example of such a mucilage, obtained from red seaweeds of the Gelidium family. Agar is a sulphuric acid ester of a galactan and is used as a gel-forming agent in media in bacteriological studies.

Pectic substances occur in the primary cell wall and intercellular layers of all land plants. They can be classified into four types: protopectin, pectin, pectic acid and pectinic acid. The fundamental structural unit in these pectic substances is galacturonic acid, although other substances have been produced on hydrolysis. Protopectin occurs in the thickening of cell walls of parenchyma, and is present in unripe fruits. Pectin is formed from protopectin by the action of the enzyme protopectinase and gives the gel-like property common to fruit juices. This property is made use of in jam-making. Pectinic and pectic acids are produced from pectin by the action of the enzyme pectase; they occur in over-ripe fruits.

LIGNIN

Lignin is not a carbohydrate, but is usually discussed along with this group of compounds because of its association with them as a structural component of the cell wall. Although the exact structure of the lignin molecule is unknown, it is thought that the basic unit is a phenylpropyl radical:



As plant tissue ages the cell walls become lignified, and it is thought that in this process cellulose and hemicelluloses combine with lignin.

Lignin is very resistant to strong acids and to microbial action. It is generally considered to be completely indigestible by animals. Mature hays and straws are of low digestibility, and this is usually associated with the presence of lignified tissues.

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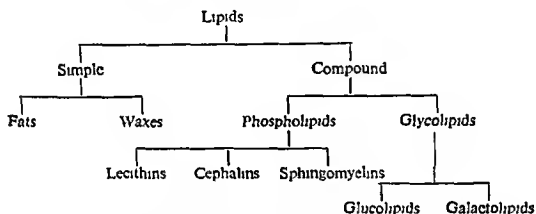
Chapter 3

LIPIDS

The lipids or lipides are a group of substances found in plant and animal tissues, insoluble in water but soluble in common organic solvents such as benzene, ether and chloroform. In the proximate analysis of foods they are included in the ether extract fraction.

The lipids may be classified into two main groups as follows:

TABLE 3.1 Classification of the Lipids



The simple lipids are esters of fatty acids with alcohols, while the compound lipids include other groups as well. For example, the phospholipids may contain choline and phosphoric acid.

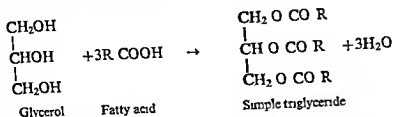
FATS

Fats and oils are constituents of both plants and animals, and are important sources of stored energy. Both have the same general structure and chemical properties but they have different physical characteristics. The melting points of the oils are such that at ordinary temperatures they are liquid. The term fat is frequently used in a general sense to include both groups.

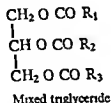
Structure of Fats

Fats are esters of fatty acids with the trihydric alcohol glycerol.

When the esterification involves only a single fatty acid, the compound produced is a simple triglyceride



When more than one fatty acid is concerned in the esterification, then a mixed triglyceride results



where $\text{R}_1, \text{R}_2, \text{R}_3$ represent the chains of different fatty acids. Naturally occurring fats and oils are mixtures of such mixed triglycerides, although simple triglycerides do occur naturally and sometimes are the dominant

TABLE 3.2 Common Acids of Natural Fats

1 Saturated fatty acids

Acid	Formula	Melting point, °C
Butyric (butanoic)	$\text{C}_3\text{H}_7\text{COOH}$	-7.9
Caproic (hexanoic)	$\text{C}_5\text{H}_{11}\text{COOH}$	-3.2
Caprylic (octanoic)	$\text{C}_7\text{H}_{15}\text{COOH}$	16.3
Capric (decanoic)	$\text{C}_9\text{H}_{19}\text{COOH}$	31.2
Lauric (dodecanoic)	$\text{C}_{11}\text{H}_{23}\text{COOH}$	43.9
Myristic (tetradecanoic)	$\text{C}_{13}\text{H}_{27}\text{COOH}$	54.1
Palmitic (hexadecanoic)	$\text{C}_{15}\text{H}_{31}\text{COOH}$	62.7
Stearic (octadecanoic)	$\text{C}_{17}\text{H}_{35}\text{COOH}$	69.6
Arachidic (eicosanoic)	$\text{C}_{19}\text{H}_{39}\text{COOH}$	76.3

2 Unsaturated fatty acids

Acid	Formula	Melting point, °C
Palmitoleic (hexadecenoic)	$\text{C}_{15}\text{H}_{29}\text{COOH}$	0
Oleic (octadecenoic)	$\text{C}_{17}\text{H}_{33}\text{COOH}$	13
Linoleic (octadecadienoic)	$\text{C}_{17}\text{H}_{31}\text{COOH}$	-5
Linolenic (octadecatrienoic)	$\text{C}_{17}\text{H}_{29}\text{COOH}$	-14.5
Arachidonic (eicosatetraenoic)	$\text{C}_{19}\text{H}_{31}\text{COOH}$	-49.5

linoleic acid, while linseed is a particularly good source of linolenic acid. Pigs and poultry, which normally have considerable amounts of oilseed residues in their diet, will therefore probably receive an adequate supply of the essential acids. Ruminants are largely dependent upon grass for their nutritional needs and are thereby supplied with considerable quantities of linoleic acid and larger quantities of linolenic acid. It is conceivable that hydrogenation of the latter in the rumen will make increased amounts of linoleic acid available, and the possibility of ruminants suffering a deficiency of essential fatty acids is, in practice, remote.

Analytical Fat Constants

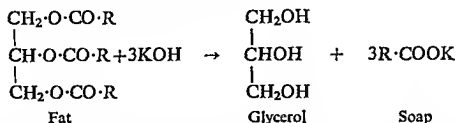
It is frequently important in nutritional investigations to assess the quality of the fat being produced under a certain treatment. Where the effect of the diet is considerable the results may be obvious in a softening or hardening of the fat. Less obvious changes may occur, and for these a more objective assessment is necessary. Differences in fats are a function of their fatty acid composition, since glycerol is common to all fats. The logical method of following changes in fats, therefore, is to measure their fatty acid constitution. Analysis of fats for individual fatty acids has presented great problems in the past, but the introduction in recent years of techniques such as gas chromatography has allowed determinations to be made more easily and accurately. As well as providing a most valuable research tool, gas chromatographic analysis has given detailed quantitative information on the fatty acid constitution of many different fats. This means a more certain identification and characterisation of fats, and provides a more accurate method of detecting and quantitatively estimating the adulteration of a given fat or oil.

Before the introduction of gas chromatography, workers used the analytical fat constants, and much of the information on fat composition is only available in this form.

Melting Point The melting points of the fatty acids increase with increase in molecular weight, while the unsaturated acids have lower melting points than their saturated analogues. The fatty acids confer their properties on the triglycerides of which they form part. A fat with a high proportion of low molecular weight fatty acids, or unsaturated acids, will have a low melting point and will be soft or even liquid at ordinary temperatures. On the other hand, a fat with a high proportion of high molecular weight saturated acids will have a high melting point and will be firm and hard. Measurement of the

melting point thus provides an indirect measure of the fatty acid composition of a fat. Unfortunately the value does not give an estimate of individual fatty acids, and also suffers from the disadvantage that the melting point is represented by a range of temperature and does not differentiate sharply between individual fats.

Saponification Value. Fats may be hydrolysed by caustic alkalis according to the following equation:



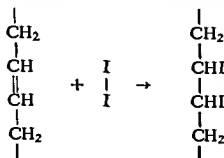
Such a hydrolysis is known as saponification since it produces soaps, which are sodium or potassium salts of fatty acids. It will be obvious that a molecule of triglyceride is always hydrolysed by the same weight of potassium hydroxide, and it follows that the actual weight of triglyceride saponified by a given weight of potassium hydroxide will vary with the molecular weight of its constituent fatty acids. Thus 302 g of tributyrin and 806 g of tripalmitin are saponified by 168 g (3 gram-molecules) of potassium hydroxide. If the amount of potassium hydroxide required to saponify a given weight of fat is determined, this will provide a measure of the molecular weight of the preponderant fatty acids present. *The saponification value is defined as the number of milligrams of potassium hydroxide required to saponify one gram of the fat.*

For tributyrin this would be $168 \times 1000/302 = 556$.

For tripalmitin it would be $168 \times 1000/806 = 208$.

Fats with a high saponification value will thus contain a high proportion of low molecular weight acids, while a low value indicates a high proportion of high molecular weight acids.

Iodine Value. The unsaturated fatty acids contain double bonds to which halogens may be added. The reaction may be represented as follows:



The amount of halogen taken up by a given fat depends upon the degree of unsaturation of its constituent acids. The use of the iodine value, defined as *the number of grams of iodine absorbed by 100 g of the fat*, is based on this concept. Oils with a high content of unsaturated acids show high values, e.g. linseed oil, 180, while those with a low unsaturated acid content have low values, e.g. coconut oil, 8.

Reichert-Meissl Value This is defined as *the number of ml of decinormal alkali required to neutralise the steam-volatile, water-soluble fatty acids from 5 g of fat*.

Butyric and caproic acids appear in this fraction *in toto*. Caprylic and capric acids also contribute to the value, but only a proportion of these acids are represented.

Butter, with a value of 20–37, is almost the only edible fat with a significant quantity of these acids, and it is in butterfat analysis that the value finds its main application. In this field it is used to assess the quality of butters produced under different conditions and in the detection of adulteration of butter with vegetable oils, which, apart from coconut oil, have values less than one.

Polenske Value This is defined as *the number of ml of decinormal alkali required to neutralise the steam-volatile, water-insoluble fatty acids from 5 g of the fat*.

The main acids contributing to this value will be capric and lauric, with minor contributions from caprylic and myristic and negligible ones from palmitic and stearic acids.

Composition of Fats

Some typical values for the various constants for different fats are given in Table 3.3.

In general the plant and marine oils, especially those of fish, are more highly unsaturated than those of mammalian origin. This is due to the presence of varying amounts of linoleic and linolenic acids in addition to the unsaturated oleic acid, which is quantitatively the major

TABLE 3.3 Analytical Constants of Some Fats and Oils

	Saponification Value	Iodine Value	Reichert Value	Polenske Value
Groundnut oil	189.196	85.98	0.4	—
Cottonseed oil	191.196	103.111	0.510	0.5
Whale oil	188.194	110–150	1.2	—
Cod oil	170–180	130–150	0.4–0.76	—
Beef tallow	190–200	32–47	0.25	1
Lard	193–200	46–66	0.70	1
Milk fat (cow)	216–238	32–42	20–37	2–4

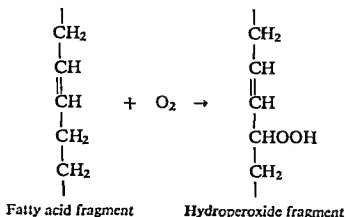
fatty acid in most natural fats. In mammalian depot fat the proportion of the more unsaturated acids is lower, and there is a higher proportion of high molecular weight saturated acids such as palmitic and stearic acids, with smaller but significant contributions from lauric and myristic acids. For this reason fats like lard, beef and mutton tallow are firm and hard, while the marine mammal, fish and plant oils are softer and are frequently oils in the true sense.

Ruminant milk fats are characterised by their high content of low molecular weight fatty acids, these sometimes forming as much as 20 per cent. of the total acids present. As a result they are softer than the depot fats of the respective animals but not as soft as fats of vegetable or marine origin, being semi-solid at ordinary temperatures. Milk fats of non-ruminants resemble the depot fat of the particular animal.

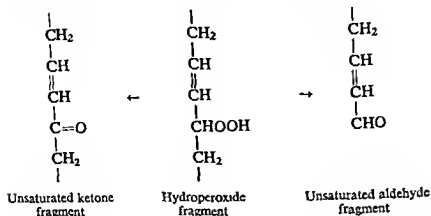
Properties of Fats

Hydrolysis. Fats may be hydrolysed by boiling with alkalis, when glycerol and soaps are formed as previously described. The process may take place naturally under the influence of the enzymes collectively known as the lipases. As a result of this lipolysis, glycerol and free fatty acids are produced. Most of these acids are odourless and tasteless, but some of the lower ones, particularly butyric and caproic, have extremely powerful tastes and smells; where such a breakdown takes place in an edible fat it may frequently be rendered completely unacceptable to the consumer. The lipases are mostly derived from bacteria and moulds, which are chiefly responsible for this type of spoilage, commonly referred to as hydrolytic rancidity.

Oxidation. The unsaturated fatty acids readily undergo oxidation, the site of action being the carbon atom adjacent to the double bond. Hydroperoxides are formed:

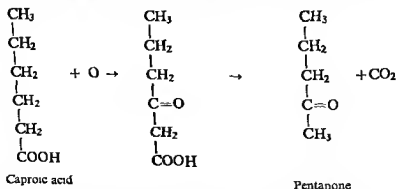


which may then break down to give unsaturated aldehydes or ketones



Such compounds, together with hydroxy-propanal, have been isolated from fats showing the so called 'oxidative' or 'oxidised' taints. No single substance has been shown to be responsible for the taints, which have been described as oily, metallic and tallowy, rather they are regarded as being due to the combined effects of the products of fat oxidation. Development of oxidative taints is accelerated by the presence of heavy metals, particularly copper and iron, and by exposure of the fat to ultra violet light.

Oxidation of saturated fatty acids results in the development of a sweet, heavy taste and smell commonly known as ketonic rancidity. This is due to the presence of methyl ketones as a result of the oxidation, which may be represented as follows

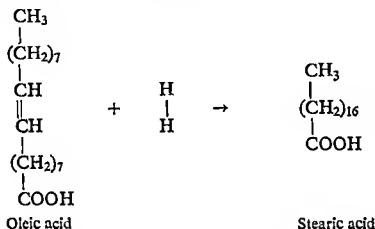


Similar reactions following mould induced lipolysis are responsible for the characteristic flavours of various soft and blue cheeses.

Antioxidants Natural fats possess a certain degree of resistance

to oxidation, owing to the presence of compounds termed antioxidants. These prevent the oxidation of unsaturated fats until they themselves have been transformed into inert products. A number of compounds have this antioxidant property, including phenols, quinones, tocopherols, gallic acid and gallates. In the United Kingdom, a Food Standard Committee reported in 1954 that it considered no health hazard should arise if 0.01 per cent. propyl, octyl or dodecyl gallate or 0.02 per cent. butylated hydroxyanisole were added to edible oils or fats.

Hydrogenation. This is the process whereby hydrogen is added to the double bonds of the unsaturated acids of a fat, converting them to their saturated analogues. Oleic acid, for example, yields stearic acid as follows:

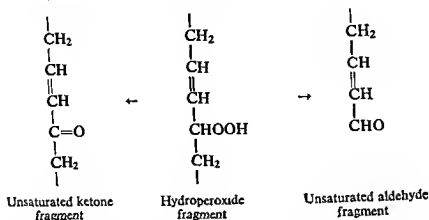


The process is important commercially for producing firm hard fats from vegetable and fish oils in the production of margarine. The hardening results from the higher melting points of the saturated acids. For the rate of reaction to be practicable a catalyst has to be used, usually finely divided nickel. Hardening has the added advantage of improving the keeping quality of the fat, since removal of the double bonds eliminates the chief centres of reactivity in the material.

WAXES

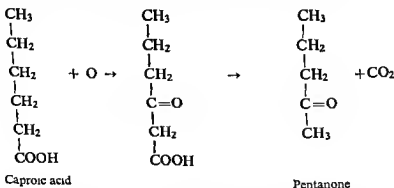
Waxes are simple lipids consisting of a fatty acid combined with a monohydric alcohol of high molecular weight. They are usually solid at ordinary temperatures. The fatty acids present in waxes are those found in fats, although acids lower than lauric are very rare while several higher acids like carnaubic ($\text{C}_{23}\text{H}_{47}\text{COOH}$) and melissic ($\text{C}_{30}\text{H}_{61}\text{COOH}$) may also be present. The most common of the alcohols found in waxes are carnaubyl ($\text{C}_{24}\text{H}_{49}\text{OH}$), myricyl ($\text{C}_{31}\text{H}_{63}\text{OH}$) and cetyl ($\text{C}_{16}\text{H}_{33}\text{OH}$).

which may then break down to give unsaturated aldehydes or ketones*



Such compounds, together with hydroxy-propanal, have been isolated from fats showing the so called 'oxidative' or 'oxidised' taints. No single substance has been shown to be responsible for the taints, which have been described as oily, metallic and tallowy, rather they are regarded as being due to the combined effects of the products of fat oxidation. Development of oxidative taints is accelerated by the presence of heavy metals, particularly copper and iron, and by exposure of the fat to ultra-violet light.

Oxidation of saturated fatty acids results in the development of a sweet, heavy taste and smell commonly known as ketonic rancidity. This is due to the presence of methyl ketones as a result of the oxidation, which may be represented as follows

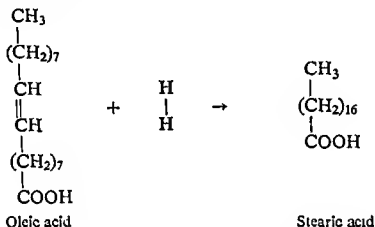


Similar reactions following mould induced lipolysis are responsible for the characteristic flavours of various soft and blue cheeses.

Antioxidants Natural fats possess a certain degree of resistance

to oxidation, owing to the presence of compounds termed antioxidants. These prevent the oxidation of unsaturated fats until they themselves have been transformed into inert products. A number of compounds have this antioxidant property, including phenols, quinones, tocopherols, gallic acid and gallates. In the United Kingdom, a Food Standard Committee reported in 1954 that it considered no health hazard should arise if 0.01 per cent. propyl, octyl or dodecyl gallate or 0.02 per cent. butylated hydroxyanisole were added to edible oils or fats.

Hydrogenation. This is the process whereby hydrogen is added to the double bonds of the unsaturated acids of a fat, converting them to their saturated analogues. Oleic acid, for example, yields stearic acid as follows:

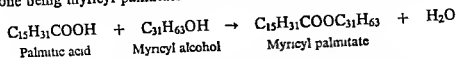


The process is important commercially for producing firm hard fats from vegetable and fish oils in the production of margarine. The hardening results from the higher melting points of the saturated acids. For the rate of reaction to be practicable a catalyst has to be used, usually finely divided nickel. Hardening has the added advantage of improving the keeping quality of the fat, since removal of the double bonds eliminates the chief centres of reactivity in the material.

WAXES

Waxes are simple lipids consisting of a fatty acid combined with a monohydric alcohol of high molecular weight. They are usually solid at ordinary temperatures. The fatty acids present in waxes are those found in fats, although acids lower than lauric are very rare while several higher acids like carnaubic ($\text{C}_{23}\text{H}_{47}\text{COOH}$) and melissic ($\text{C}_{30}\text{H}_{61}\text{COOH}$) may also be present. The most common of the alcohols found in waxes are carnaubyl ($\text{C}_{24}\text{H}_{49}\text{OH}$), myricyl ($\text{C}_{31}\text{H}_{63}\text{OH}$) and cetyl ($\text{C}_{16}\text{H}_{33}\text{OH}$).

Natural waxes are usually mixtures of a number of different esters. Beeswax is known to consist of at least five different esters, the main one being myrcyl palmitate



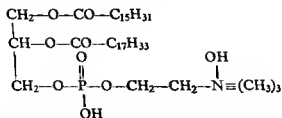
Waxes are widely distributed in plants and animals, where they often have a protective function. In plants water losses due to transpiration are reduced, and in animals wool and feathers are protected against water by the hydrophobic nature of the wax coating. Among the better-known animal waxes are lanolin, obtained from wool, and spermaceti, a product of marine animals. Unlike fats, waxes are not readily hydrolysed and are unlikely to have any nutritive value. Their presence in foods in large amounts leads to a high ether extract figure and may result in the nutritive value being overestimated.

COMPOUND LIPIDS

Phospholipids

These are widely distributed in all living tissues, notably in the heart, brain and kidneys. Eggs are one of the best animal sources, while among the plants soya beans contain relatively large amounts. The phospholipids contain nitrogen and phosphorus in addition to carbon, hydrogen and oxygen, and are of three types, viz. the lecithins, the cephalins and the sphingomyelins. The first two are closely related structurally and in behaviour, but the sphingomyelins form a separate and distinct group.

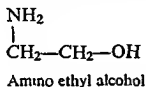
Lecithins, like the fats, are all esters of glycerol. Two of the alcohol groups are esterified with fatty acids, but the third is esterified with phosphoric acid, which is in turn esterified by the nitrogenous base, choline. A typical lecithin would be



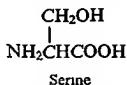
The chief fatty acids present are palmitic, stearic, arachidic and oleic. Acids below lauric are not found in the lecithins.

The lecithins are white waxy solids which quickly turn brown in the air owing to oxidation. They characteristically exhibit a dual nature since they are intensely hydrophilic as well as being typically lipid. Naturally occurring enzymes, the lecithinases, are capable of hydrolysing the lecithins, yielding fatty acids, glycerophosphates and choline. The release of choline, when followed by a further oxidative breakdown, has been considered to be responsible for the development of fishy taints in fats through the release of the trimethylammonium group or its oxide, but currently these taints are considered to be the result of fat oxidation and not of lecithin breakdown.

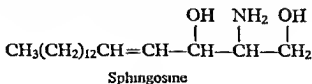
Cephalins differ from the lecithins in having cholamine as their nitrogenous base. Cholamine is amino ethyl alcohol



The amino acid serine may sometimes be present



Sphingomyelins do not contain glycerol and are made up of fatty acids, phosphoric acid, choline and sphingosine, which has the following formula



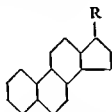
Glycolipids

The glycolipids have been referred to as the cerebroside because of their occurrence in brain tissue. In the brain they contain either galactose or glucose, combined with a fatty acid and sphingosine. Those containing glucose are known as glucolipids and those containing galactose as galactolipids. Galactolipids also occur in plants, and it has recently been shown that the neutral lipids of clover contain about 60 per cent of galactolipids. Acid hydrolysis of these compounds produces glycerol, galactose and fatty acids (mainly linolenic acid).

STEROLS

In addition to those substances already discussed, the ether extract fraction contains an unsaponifiable component, the sterols. These compounds are unsaturated monohydric alcohols of high molecular weight which occur in all living cells, either in the free state or combined with fatty acids as esters

Sterols all have the same basic structural unit of a phenanthrene nucleus linked to a cyclopentane ring



The different sterols vary in the number and position of the double bonds and the nature of the side-chain R. This basic cyclic structure occurs in the bile acids, the sex hormones, the adrenal hormones and the D vitamin precursors

The sterols may be classified into

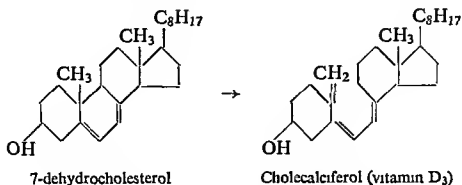
- (a) the phytosterols of plant origin,
- (b) the mycosterols of fungal origin,
- (c) the zoosterols of animal origin

The phytosterols and the mycosterols are not absorbed from the gut and are not found in animal tissues

Cholesterol is a zoosterol which is quantitatively an important constituent of the brain, where it may form up to 17 per cent of the dry matter. It occurs in smaller amounts in all animal cells and it can be synthesised in the body, but, in spite of this wide distribution and apparent importance, little is known of its actual function. Many of the important sterols of the body may be synthesised from cholesterol, and many consider that its function is to act as a source material in such syntheses. It has attained some prominence in recent years in connection with the condition of atherosclerosis, which involves a thickening of the arterial walls. The thickening is due to deposits containing cholesterol which form on the inside of the arterial walls.

7 dehydrocholesterol, which is derived from cholesterol, is important

as the precursor of vitamin D₃, which is produced when the sterol is exposed to ultra-violet light



This is a good illustration of how relatively small changes in chemical structure may bring about radical changes in physiological activity

Ergosterol is a phytosterol widely distributed in brown algae, bacteria and higher plants. It is important as the precursor of ergocalciferol or vitamin D₂, into which it is converted by ultra-violet irradiation. The change is the same as that which takes place in the formation of vitamin D₃ from 7-dehydrocholesterol and involves opening of the second phenanthrene ring.

FURTHER READING

- H. J. DEUEL, 1951 *The Lipids: their Chemistry and Biochemistry* Interscience Publishers, New York
- T. P. HILDITCH AND P. N. WILLIAMS, 1964 *The Chemical Constitution of Natural Fats*, 4th ed. Chapman and Hall, London
- M. M. RAPPORT AND W. T. NORTON, 1962 *Chemistry of the lipids Annual Review of Biochemistry*, 31, 103-138
- F. D. GUNSTONE, 1958 *An Introduction to the Chemistry of Fats and Fatty Acids* Chapman and Hall, London

Chapter 4

PROTEINS

Proteins are complex organic compounds of high molecular weight. In common with carbohydrates and fats they contain carbon, hydrogen and oxygen, but in addition they all contain nitrogen and generally sulphur.

Proteins are found in all living cells, where they are intimately connected with all phases of activity that constitute the life of the cell. Each species has its own specific proteins, and it should be noted that a single organism has many different proteins in its cells and tissues. It follows therefore that a large number of proteins occur in nature.

AMINO ACIDS

Amino acids are produced when proteins are hydrolysed by enzymes, acids or alkalis. Although over a hundred amino acids have been isolated from biological materials, only 25 of these are generally regarded as being components of proteins.

Amino acids are characterised by having a basic nitrogenous group, generally an amino group ($-\text{NH}_2$), and an acidic carboxyl unit ($-\text{COOH}$). Most amino acids occurring naturally in proteins are of the α type, having the amino group attached to the carbon atom adjacent to the carboxyl group, and can be represented by the general formula



The two exceptions are proline and hydroxyproline, which have an imino (NH) instead of an amino group (Table 4.1). Some amino acids have additional amino and/or carboxyl groups.

Properties of Amino Acids

Because of the presence of an amino and a carboxyl group, amino

acids are amphoteric, i.e. have both basic and acidic properties. Molecules such as these, with basic and acidic groups, might exist as uncharged molecules, or as dipolar ions with opposite ionic charges, or as a mixture of these. Amino acids exist as dipolar ions or 'zwitter ions' (from the German *Zwitter*, a hermaphrodite)

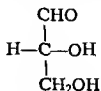


In a strongly acid solution an amino acid exists largely as a cation, while in alkaline solution it occurs mainly as an anion. There is a pH value for a given amino acid at which it is electrically neutral, this value is known as the *isoelectric point*.

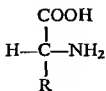
Because of their amphoteric nature amino acids act as buffers, resisting changes in pH. All the α -amino acids except glycine are optically active.

The nature of the 'R' group varies with different amino acids. It may simply be a hydrogen atom as in glycine, or it may be a more complex radical containing, for example, a phenyl group. Table 4.1 lists the important amino acids derived from proteins. Most of these amino acids are of general occurrence in proteins, although diiodotyrosine, hydroxylysine, hydroxyproline and thyroxine occur in only a few.

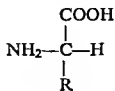
All the amino acids involved in protein structure have an L-configuration of the carbon atom. Configurations are determined by relation to the standard substance D glycerose, as described under Carbohydrates (Chapter 2).



D Glycerose



D Amino acid



L Amino acid

Essential Amino Acids

Plants and many micro-organisms are able to synthesise proteins from simple nitrogenous compounds such as nitrates. Animals cannot synthesise the amino group, and in order to build up body

TABLE 4 1. Amino Acids Occurring as Protein Structure Units

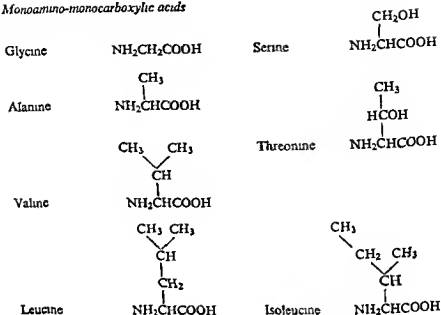
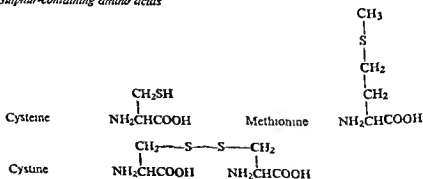
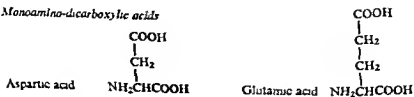
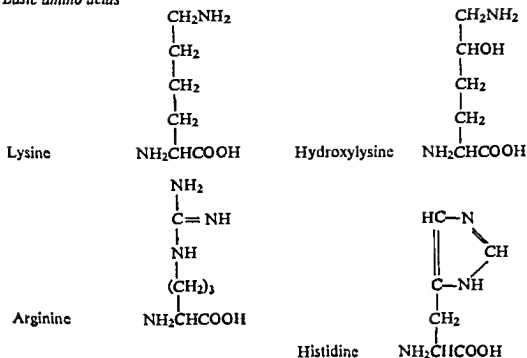
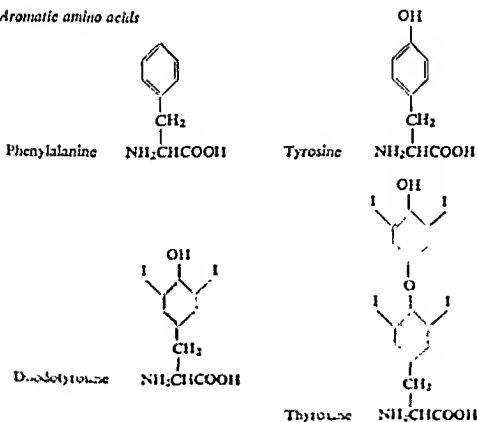
1. *Monoamino-monocarboxylic acids*2. *Sulphur-containing amino acids*3. *Monoamino-dicarboxylic acids*

TABLE 4.1.—*Continued*

4. *Basic amino acids*



5. *Aromatic amino acids*



however that the term 'molecular weight' in protein chemistry can be misleading, since some proteins in aqueous solutions exist as polymers but dissociate into monomers when the solution is diluted or when the pH or the temperature is altered

PROPERTIES OF PROTEINS

All proteins are of high molecular weight, and have colloidal properties

Proteins differ in their solubility in water, ranging from insoluble keratin to albumins which are highly soluble. Soluble proteins can be precipitated from solution by the addition of certain salts such as sodium chloride or ammonium sulphate. This is a physical effect and the properties of the proteins are not altered. On dilution the proteins can easily be redissolved.

Although the amino and carboxyl groups in the peptide linkage are non functional to acid base reactions, all proteins contain a number of free amino and carboxyl groups, either as terminal units or in the side-chain of amino acid residues. Like amino acids, proteins are therefore amphoteric. They exhibit characteristic isoelectric points, and have buffering properties.

All proteins can be *denatured* or changed from their natural state. Denaturation has been more accurately defined by Neurath and co-workers as 'any nonproteolytic modification of the unique structure of a native protein, giving rise to definite changes in chemical, physical or biological properties'. Products of protein hydrolysis are not included under this term. Perhaps the best example of denaturation is the coagulation of a protein solution, such as egg white, upon heating. Many proteins are heat-coagulable. Apart from heat there are many other agents which can bring about the denaturation of proteins, these include strong acid, alkali, alcohol, acetone, urea, and salts of heavy metals.

The most notable effects of denaturation are the changes in biological properties, for example enzymes are usually inactivated. Changes in solubility and optical activity may also occur. Solutions of proteins are laevo-rotatory, and denaturation increases the specific rotation.

CLASSIFICATION OF PROTEINS

Proteins are conveniently classified into three main groups: simple, conjugated and derived proteins. Simple proteins produce only amino

acids or their immediate derivatives on hydrolysis. The conjugated, or compound, proteins on hydrolysis yield non-protein groups, usually called 'prosthetic' groups, as well as amino acids. The third group contains denatured proteins and products derived from proteins by partial hydrolysis.

Simple Proteins

This group includes albumins, which are water-soluble and heat-coagulable and occur in eggs, milk and blood. The globulins, insoluble in water and heat-coagulable, are present in eggs, milk and blood and are the main reserve proteins in seeds. Lactoglobulin is a protein of milk; it was at first considered to be a homogenous protein, but actually consists of two components designated A and B lactoglobulin. Individual cows contain either one or the other or both, depending upon genetic factors.

The glutelins are insoluble in water and are not heat-coagulable. These simple proteins, together with gliadins which have similar properties, make up the main proteins found in endosperm proteins of cereal grains. Histones are water-soluble but not heat-coagulable, and on hydrolysis produce large quantities of histidine and lysine. Scleroproteins are very insoluble and occur only in animals; they make up the skeletal, epidermal and connective tissues. Finally the protamines are the simplest natural proteins and occur in fish sperm; they are water-soluble but are not coagulated by heat.

Conjugated Proteins

The prosthetic group present in conjugated proteins varies and may be phosphoric acid (phosphoproteins), hexose or a hexose derivative (glycoproteins), a pigment (chromoproteins) or a nucleic acid (nucleoproteins).

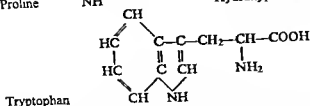
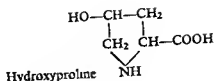
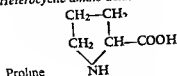
Casein of milk and phosvitin present in egg yolk are phosphoproteins containing phosphoric acid, which is believed to be linked to the β -hydroxyl group of serine and threonine residues. Mucin, the main component of the secretion mucus, is a glycoprotein. Haemoglobin is an important chromoprotein, consisting of the protein, globin, combined with an iron-containing compound, haem or haematin.

Considerable attention has recently been given to nucleic acids, the prosthetic groups of nucleoproteins, and these will be dealt with in some detail here.

Nucleic acids. Nucleic acids are high molecular weight compounds which on hydrolysis yield pentose sugars, nitrogenous bases and

TABLE 41—Continued

6 Heterocyclic amino acids



proteins they must have a dietary source of amino acids. Certain amino acids can be produced from others by a process known as *transamination* (see Chapter 9), but a number cannot be effectively synthesised in the animal body and these are referred to as 'essential amino acids'.

Most of the early work in determining the amino acids which could be classed as 'essential' was carried out with rats fed on purified diets. The following ten essential amino acids are required for growth in the rat.

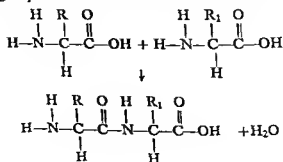
Arginine
Histidine
Isoleucine
Leucine
Lysine

Methionine
Phenylalanine
Threonine
Tryptophan
Valine

Essential amino acids are also important in the nutrition of farm animals. The biological significance of this is discussed in Chapter 13.

STRUCTURE OF PROTEINS

It is generally accepted that proteins are built up from amino acids by means of a linkage between the α carboxyl of one amino acid and the α amino group of another acid.



This type of linkage is known as the peptide linkage; in the example on p. 38 a dipeptide has been produced from two amino acids. Large numbers of amino acids can be joined together by this means with the elimination of one molecule of water at each linkage.

It was originally proposed, by both Fischer and Hofmeister at the beginning of this century, that proteins were essentially polypeptides containing many amino acid residues joined together by means of the peptide linkage. This theory is still regarded as the most satisfactory, although the conception of a simple, long, straight chain of amino

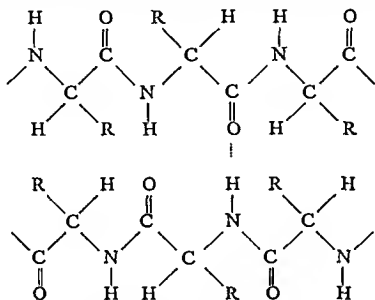


FIG. 4.1. Configuration of polypeptide chain. Dotted lines represent possible hydrogen bonds.

acid residues does not explain many of the properties of natural proteins. A more complex type of structure is visualised, in which separate polypeptide chains may be cross-linked by means of linkages other than the peptide bond. Proteins containing cysteine residues may possess a disulphide linkage (—S—S—) between two cysteine residues. Ester linkages between the alcoholic groups of amino acid side-chains with carboxyl groups have been suggested, as well as salt linkages in which free amino units in one side-chain combine with free carboxyl units in another chain. Hydrogen bonds may also act as intramolecular bonding forces, as illustrated in Fig. 4.1.

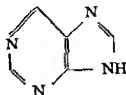
It is clear from a knowledge of the molecular weights of certain proteins that the actual structure of the molecule must be extremely complex. Most proteins have molecular weights varying from 20,000 to 200,000, although virus proteins, which may have molecular weights running into several millions, are exceptions. It should be pointed out

phosphoric acid. They can be divided into two general types depending upon the constituent sugar present. ribonucleic acid (RNA) contains ribose, while deoxyribonucleic acid (DNA) contains the ribose derivative, deoxyribose. DNA is always found in the cell nucleus, RNA mainly in the cytoplasm.

The nitrogenous components are derivatives of pyrimidine or purine.



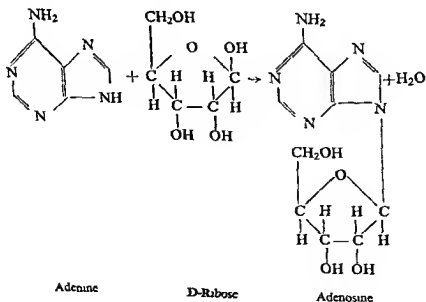
Pyrimidine



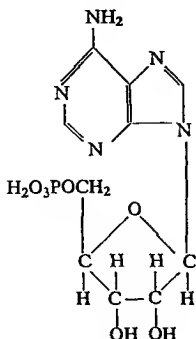
Purine

The two nucleic acids also differ in the types of bases present. DNA contains the purines, adenine and guanine, and the pyrimidines, cytosine and thymine. RNA contains the pyrimidine, uracil, in place of thymine. Very small quantities of other pyrimidines have been isolated from DNA.

The compound produced by linking a nitrogenous base to a pentose is termed a nucleoside, e.g.



If nucleosides such as adenosine are esterified with phosphoric acid, they form nucleotides, e.g.



Adenosine 5'-phosphate (adenylic acid)

Nucleic acids are polynucleotides of very high molecular weight, generally measured in several millions. The nucleotides are arranged in a certain pattern—DNA normally consists of a double-strand spiral (Fig. 4.2). Each strand consists of alternate units of the deoxyribose and phosphate groups. Attached to each sugar group is one of the four bases mentioned above. The bases on the two strands of the spiral are joined in pairs by hydrogen bonds, the thymine on one strand always being paired with the adenine on the other and the cytosine with guanine. The sequence of bases along these strands is believed to carry the genetic information of the living cell.

Present evidence indicates that RNA exists in the form of single, long, folded chains arranged spirally. RNA usually occurs combined with proteins, and can exist in four different forms: nuclear RNA, ribosomal RNA, transfer RNA and messenger RNA. These play an important part in the synthesis of proteins (see Chapter 9).

Derived Proteins

This term has been used to describe the products obtained from proteins by denaturation or partial degradation. In the older biochemical literature terms such as proteoses and peptones were used to describe the products from partial hydrolysis of proteins, but those

terms are now considered to be unsatisfactory since the compounds to which they refer are probably mixtures of peptides of differing molecular size and structure

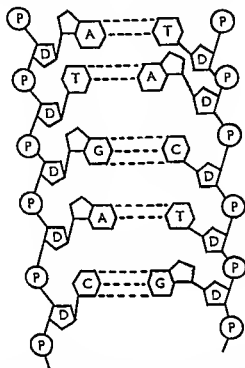


FIG 4.2 Diagrammatic representation of part of the ladder like DNA molecule, showing the two strands of alternate phosphate (P) and deoxyribose (D) molecules. The horizontal rods represent the pairs of bases held by hydrogen bonds (represented by dotted lines)

A = Adenine T = Thymine C = Cytosine G = Guanine

NON PROTEIN NITROGENOUS COMPOUNDS

A considerable variety of nitrogenous compounds which are not classed as proteins occur in plants and animals. In plant analysis these compounds have been frequently classed together as non protein nitrogenous compounds, to distinguish them from 'true proteins' determined in routine chemical analysis. Amino acids form the main part of the non protein nitrogenous fraction in plants, and those present in greatest amount include glutamic acid, aspartic acid, alanine, serine, glycine and proline. Other compounds are nitrogenous lipids, amines, amides, purines, pyrimidines, nitrates and alkaloids. In

addition many members of the vitamin B complex contain nitrogen in their structure.

It is clearly impossible to deal with these compounds in any detail, and only some of the important ones not previously mentioned will be discussed. Table 4.2 shows the main non-protein nitrogenous components of two herbage samples.

TABLE 4.2. Composition of Non-Protein Nitrogen (NPN) of two Herbages (After W. S. Ferguson and R. A. Terry, 1954, *J. Sci. Fd Agric.*, 5, 515)

	<i>Perennial ryegrass: percentage of NPN</i>	<i>White clover: percentage of NPN</i>
Amino-N	46.6	49.8
Amide-N	9.7	13.0
Ammonia-N	3.2	2.6
Nitrate-N	7.9	3.9
Purine-N	7.5	6.7
Betaine-N	1.9	1.0
Choline-N	1.8	0.8

Amines. Amines are basic compounds present in small amounts in most plant and animal tissues. Many occur as decomposition products in decaying organic matter and have toxic properties.

A number of micro-organisms are capable of producing amines by decarboxylation of amino acids. These may be produced in the rumen under certain conditions and may give rise to physiological

TABLE 4.3. Some Important Amines and their Parent Amino Acids

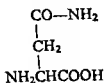
<i>Amino acid</i>	<i>Amine</i>
Arginine	Putrescine
Histidine	Histamine
Lysine	Cadaverine
Phenylalanine	Phenylethylamine
Tyrosine	Tyramine
Tryptophan	Tryptamine

symptoms; histamine, for example, is an amine formed from the amino acid, histidine, and in cases of anaphylactic shock is found in the blood in relatively large amounts. Table 4.3 gives a list of the important amines formed from amino acids.

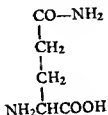
Betaine is a tertiary amine which is formed by the oxidation of choline. Betaine occurs in sugar beet, and the young leaves may contain 2.5 per cent.; it is this amine which is responsible for the

'fishy' aroma frequently associated with the commercial extraction of sugar from beet. In the animal body betaine may be transformed into trimethylamine, and it is this which gives the fishy taint to milk produced by cows that have been given excessive amounts of sugar beet by products.

Amides Asparagine and glutamine are important amide derivatives of the amino acids, aspartic acid and glutamic acid. These two amides may themselves be classed as amino acids, as can be seen from their formulae



Asparagine



Glutamine

Asparagine and glutamine may occur as components of proteins, they certainly occur as free amides and play an important role in transamination reactions.

Urea is an amide which is the main end product of nitrogen metabolism in mammals, although it also occurs in many plants and has been detected in wheat, soya bean, potato and cabbage.



Urea

Nitrates Nitrates may be present in plant materials, and while nitrate itself may not be toxic to animals it is reduced readily under favourable conditions, as in the rumen, to nitrite, which is toxic. 'Oat hay poisoning' is attributed to the relatively large amount of nitrate present in green oats.

Quite high levels of nitrate have been reported in herbage given heavy dressings of nitrogenous fertilisers (see Chapter 16).

Alkaloids These compounds occur only in certain plants, and are of particular interest since many of them have poisonous properties. Their presence is restricted to a few orders in the dicotyledons. A

number of the more important alkaloids, with their sources, are listed in Table 4 4.

TABLE 4 4 Some Important Alkaloids occurring in Plants

<i>Name</i>	<i>Source</i>
Coniine	Hemlock
Nicotine	Tobacco
Ricinine	Castor plant seeds
Atropine	Deadly nightshade
Cocaine	Leaves of coca plant
Jacobine	Ragwort
Quinine	Cinchona bark
Strychnine	Seeds of <i>Nux vomica</i>
Morphine	Dried latex of opium poppy
Solanine	Unripe potatoes and potato sprouts

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Chapter 5

VITAMINS

The discovery and isolation of many of the vitamins was originally achieved through work on rats which had been given diets of purified proteins, fats, carbohydrates and inorganic salts. Using this technique, Hopkins in 1912 showed that a synthetic diet of this type was inadequate for the normal growth of rats, but that when a small quantity of milk was added to the diet the animals developed normally. This proved that there was some essential factor, or factors, lacking in the pure diet.

About this time the term 'vitamines', derived from 'vital amines', was coined by Funk to describe these accessory food factors, which he thought contained amino-nitrogen. It is now known that only a few of these substances contain amino nitrogen and the word has been shortened to vitamins, a term which has been generally accepted as a group name.

Although the discovery of the vitamins dates from the beginning of the twentieth century, the association of certain diseases with dietary deficiencies has been known for some time. In 1753 Lind, a British naval physician, published a treatise on scurvy proving that this disease could be prevented in human beings by including salads and summer fruits in their diet. The action of lemon juice in curing and preventing scurvy had been known, however, since the beginning of the seventeenth century. The use of cod liver oil in preventing rickets has long been appreciated, and Eijkmann knew at the end of the last century that beriberi, a disease common in the Far East, could be cured by giving the patients brown rice grain as distinct from polished rice.

Vitamins are frequently defined as organic compounds which are required in small amounts for normal growth and maintenance of animal life. But this definition ignores the important part that these chemical substances play in plants, and their importance generally in the metabolism of all living organisms.

Vitamins are required by animals in very small amounts compared

with other nutrients, for example, the vitamin B₁ (thiamine) requirement of a 100 lb pig is only 2.6 mg per day. Yet a continuous deficiency in the diet results in disordered metabolism and eventually disease.

Some compounds function as vitamins only after undergoing a chemical change, such compounds, which include β carotene and certain sterols, are described as provitamins or vitamin precursors.

Many vitamins are destroyed by oxidation, a process speeded up

TABLE 5.1 Vitamins Important in Animal Nutrition

<i>Vitamin</i>	<i>Chemical name</i>
<i>Fat soluble vitamins</i>	
A	retinol
D ₂	ergocalciferol
D ₃	cholecalciferol
E	α tocopherol *
K	phyloquinone †
<i>Water soluble vitamins</i>	
B complex	
B ₁	thiamine
B ₂	riboflavin
	nicotinamide
B ₆	pyridoxine
	pantothenic acid
	biotin
	folic acid
	choline
B ₁₂	cyanocobalamin
C	ascorbic acid

* A number of tocopherols have vitamin E activity

† Several naphthoquinone derivatives possessing vitamin K activity are known

by the action of heat, light and certain metals such as iron. This fact is important since the conditions under which a food is stored will affect the final vitamin potency. Some commercial vitamin preparations are dispersed in wax or gelatin, which act as a protective layer against oxidation.

The system of naming the vitamins by letters of the alphabet was most convenient and was generally accepted before the discovery of their chemical nature. Although this system of nomenclature is still widely used with some vitamins, the modern tendency is to use the chemical name, particularly in describing members of the B complex.

There are at least 15 vitamins which have been accepted as essential food factors, and a few others have been proposed. Not all of them

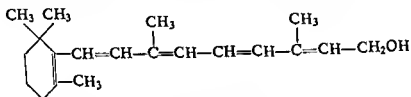
are of practical importance, and only those vitamins which may be deficient in the diets of farm animals are dealt with in this chapter.

It is convenient to divide the vitamins into two main groups, the water-soluble and the fat-soluble. Table 51 lists the important members of these two groups.

VITAMIN A

Chemical Nature

Vitamin A, known chemically as retinol, is an unsaturated monohydric alcohol with the following structural formula



Vitamin A ($C_{20}H_{29}OH$)

The vitamin is a pale yellow crystalline solid, insoluble in water but soluble in fat and various fat solvents. It is readily destroyed by oxidation on exposure to air and light. A related compound with the formula $C_{20}H_{27}OH$, found in fish, has biological activity much lower than that of vitamin A and has been designated dehydroretinol or vitamin A_2 .

Sources

Vitamin A accumulates in the liver and therefore this organ is likely to be a rich source, this is particularly true in the case of certain fish, cod liver oil and halibut liver oil being excellent sources. Egg yolk and milk fat are also generally regarded as being rich sources, although the amount in these depends to a large extent upon the diet of the animals by which they have been produced.

Vitamin A is manufactured synthetically and can be obtained in a pure form.

Provitamins Vitamin A does not exist as such in plants, but is present as precursors or provitamins in the form of certain carotenoids which can readily be converted by the animal into the vitamin. These carotenoids include α -, β - and γ -carotenes, cryptoxanthin which is present in higher plants, and myxoxanthene which occurs in a blue-green alga. Of these β -carotene is the most widely distributed, and since its vitamin A activity is considered to be greater than that of the

Metabolism

The full part played by vitamin A in the metabolic processes is still obscure, although it has been suggested that it is concerned with hydrogen transference. Rhodopsin (visual purple), the pigment of the rod cells of the retina of the eye, is made up of the vitamin *plus* a protein moiety. The pigment breaks down into its constituents when exposed to light and these chemical changes are accompanied by stimulation of the optic nerves. In the dark rhodopsin is regenerated.

Ability to see in dim light depends upon the rate of resynthesis of rhodopsin, and where vitamin A is deficient rhodopsin formation is impaired. One of the earliest symptoms of a deficiency of vitamin A is a lessened ability to see in dim light, commonly known as night blindness. This is a symptom in all animals.

The vitamin is also concerned with maintaining the mucous membranes of the respiratory tract, intestinal tract, urethra, kidneys and eyes in healthy condition. In its absence they become keratinised and dried out, in which condition they are very susceptible to infection. In addition vitamin A has a role in bone formation.

Deficiency Symptoms

In adult cattle a mild deficiency of vitamin A is associated with roughened hair and scaly skin. If it is prolonged the eyes are affected, leading to excessive watering, softening and cloudiness of the cornea and development of xerophthalmia, characterised by a drying of the conjunctiva. Constriction of the optic nerve canal may result in blindness in calves. In breeding animals a deficiency may lead to infertility, and in pregnant animals to abortion or to the production of dead, weak or blind calves. Less severe deficiencies may result in calves born with low reserves of the vitamin, and it is imperative that colostrum, rich in antibodies and vitamin A, should be given at birth, otherwise the susceptibility of such animals to infection leads to scours, and if the deficiency is not rectified they frequently die of pneumonia.

In practice severe deficiency symptoms are unlikely to occur in adult animals except after prolonged deprivation. Grazing animals generally obtain more than adequate amounts of provitamin from pasture grass and normally build up liver reserves. If cattle are fed on silage or well preserved hay during the winter months, deficiencies are unlikely to occur. Cases of vitamin A deficiency have been reported among cattle fed indoors on high cereal rations, and under these conditions a high vitamin supplement is recommended.

In ewes, in addition to night blindness, severe cases of deficiency may result in lambs being born weak or dead. A deficiency is not common in sheep, however, because of adequate dietary intakes on pasture.

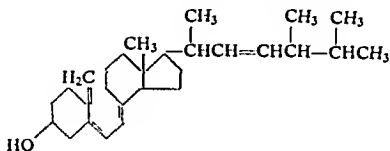
In pigs, eye disorders such as xerophthalmia and blindness may occur. A deficiency in pregnant animals may result in the production of blind, deformed litters. In less severe cases appetite is impaired and growth retarded. Where pigs are reared out of doors and have access to green food, deficiencies are unlikely to occur except possibly during the winter. Pigs kept indoors on concentrates may not receive adequate amounts in the diet and a vitamin A supplement may be required.

In poultry on a diet deficient in vitamin A, the mortality rate is usually high. Early symptoms include retarded growth, weakness, ruffled plumage and a staggering gait. In mature birds egg production and hatchability are reduced. Since most concentrated foods present in the diets of poultry are low or lacking in vitamin A or its precursors, vitamin A deficiency may be a problem unless precautions are taken. Yellow maize, dried grass or other green food, or alternatively cod or other fish liver oils or vitamin A concentrate, can be added to the diet.

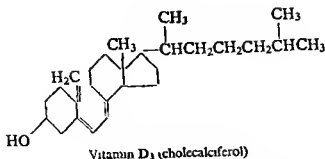
VITAMIN D

Chemical Nature

At least ten different forms of vitamin D are known, although not all of these are naturally occurring compounds. The two most important forms are ergocalciferol (D_2) and cholcalciferol (D_3). The term D_1 was originally suggested by the earlier workers for an activated sterol which was found later to be impure and to consist mainly of ergocalciferol, which had already been designated D_2 . The result of this confusion is that in the group of D-vitamins the term vitamin D_1 has been abolished. The structures of vitamins D_2 and D_3 are as follows:



Vitamin D_2 (ergocalciferol)



The D-vitamins are insoluble in water but soluble in fats and fat solvents. Both D₂ and D₃ are more stable to oxidation than vitamin A, D₃ being more stable than D₂.

Sources

The D vitamins are limited in distribution. They rarely occur in plants except in sun dried roughages and the dead leaves of growing plants. In the animal kingdom vitamin D₃ occurs in small amounts in certain tissues, and is abundant only in some fishes. Halibut liver and cod liver oils are rich sources of vitamin D₃. Egg yolk is also a good source, but cows' milk is normally a poor source, although summer milk tends to be richer than winter milk. Colostrum usually contains from 6 to 10 times the amount present in ordinary milk.

Provitamins Reference has been made (Chapter 3) to two sterols, ergosterol and 7 dehydrocholesterol, as being precursors of vitamins D₂ and D₃ respectively. The provitamins, as such, have no vitamin value and must be converted into calciferols before they are of any use to the animal. For this conversion it is necessary to impart a definite quantity of energy to the sterol molecule, and this can be brought about by the ultra violet light present in sunlight, by artificially produced radiant energy or by certain kinds of physical treatment. Under natural conditions activation is brought about by irradiation from the sun. The activation occurs most efficiently with light of wavelength between 280 and 297 mμ, so that the range capable of vitamin formation is small. The amount of ultra violet radiation which reaches the earth's surface depends upon latitude and atmospheric conditions. The presence in the atmosphere of clouds, smoke and dust reduces the radiation. Ultra violet radiation is greater in the tropics than in the temperate regions, and the amount reaching the more northern areas in winter may be slight. Since ultra violet light cannot pass through ordinary window glass, animals housed indoors receive little suitable radiation, if any, for the production of the vitamin. Irradiation is

apparently more effective in animals with light-coloured skins. If irradiation is continued for a prolonged period, then the vitamin may itself be altered to compounds which can be toxic.

The chemical transformation occurs in the skin and also in the skin secretions, which are known to contain the precursor. Absorption of the vitamin can take place from the skin, since rickets can be treated successfully by rubbing cod liver oil into the skin.

Vitamin D requirements are usually expressed in terms of International Units (I.U.). One I.U. of vitamin D is defined as the vitamin D activity of 0.025 μg of crystalline vitamin D_3 .

Metabolism

The exact biochemical action of vitamin D in the animal is not known, although it appears to facilitate the deposition of calcium and phosphorus in bones and to increase the absorption of these elements from the intestine. The vitamin is also thought to be concerned in citrate metabolism.

Deficiency Symptoms

A deficiency of vitamin D in the young animal results in rickets, a disease of growing bone in which the deposition of calcium and phosphorus is disturbed; as a result the bones are weak and easily broken and the legs may be bowed. In young cattle the symptoms include swollen knees and hocks and arching of the back. In pigs the symptoms are usually enlarged joints, broken bones, stiffness of the joints and occasionally paralysis. The growth rate is generally adversely affected. The term 'rickets' is confined to young growing animals; in older animals vitamin D deficiency causes osteomalacia, in which there is reabsorption of bone already laid down. Osteomalacia due to vitamin D deficiency is not common in farm animals, although a similar condition can occur in pregnant and lactating animals, who require increased amounts of calcium and phosphorus. Rickets and osteomalacia are not specific diseases necessarily caused by vitamin D deficiency, but can be caused by lack of calcium or phosphorus or an imbalance between these two elements.

In poultry, a deficiency of vitamin D causes the bones and beak to become soft and rubbery; growth is usually retarded and the legs may become bowed. Egg production may also be reduced. Most foods of pigs and poultry, with the possible exception of fish meal, contain little or no vitamin D, and the vitamin is generally supplied to

these animals, if reared indoors, in the form of fish liver oils or synthetic preparations

The need for supplementing the diets of cattle and sheep with vitamin D is probably not so great as that for pigs and poultry. Adult ruminants can receive adequate amounts of the vitamin from hay in the winter months, and from irradiation while grazing. However, since the vitamin D content of hays is extremely variable, it is possible that vitamin D supplementation may be desirable, especially with young growing animals or pregnant animals on winter diets. But there is a considerable lack of information about the vitamin D needs of farm animals under practical conditions.

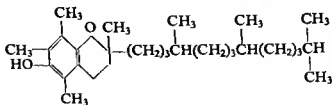
Vitamins D₂ and D₃ have the same potency for cattle, sheep and pigs, but vitamin D₂ has only about 1/35th of the potency of D₃ for poultry

In New Zealand and Southern Australia young sheep whose growth is retarded during winter months respond to vitamin D administration. An anti-vitamin D factor is suspected, because vitamin D, calcium and phosphorus intakes are generally normal. Carotene is known to have anti-vitamin D activity, although it is thought that there may be other factors in herbage concerned in the aetiology of this condition

VITAMIN E

Chemical Nature

Vitamin E is a group name which includes a number of closely related active compounds known chemically as tocopherols. Seven naturally occurring active forms of tocopherol are known, of these α tocopherol is the most active and is more widely distributed than the other forms. The formula for this compound is given below



α -Tocopherol

Sources

Vitamin E is very widely distributed in foods. The best-known sources are green leaves and cereal grains, the vitamin being concentrated in the embryo of the grain. The amount of the vitamin present

in animal products is related to the level of vitamin E in the diet, and hence is very variable. Synthetic α -tocopherol and the acetate are available as commercial preparations.

The vitamin E values of foods are stated in terms of International Units, one I U of vitamin E being defined as the specific activity of 1 mg of synthetic racemic α -tocopherol acetate.

Metabolism

Although the exact biological function of vitamin E is uncertain, it is thought to be concerned in many enzyme systems. It has been suggested that vitamin E may function

- 1 as a biological anti-oxidant,
- 2 in normal tissue respiration,
- 3 in normal phosphorylation reactions,
- 4 in metabolism of nucleic acids,
- 5 in synthesis of ascorbic acid,
- 6 in synthesis of ubiquinone (coenzyme Q)

Deficiency Symptoms

Early experiments carried out with rats on vitamin E deficient diets showed that the animals failed to reproduce. These experiments led to the vitamin being originally termed the anti sterility vitamin. This term however is misleading and is no longer used, since reproductive failures do not occur in all species when the vitamin is deficient. Table 5.2 lists some of the conditions associated with vitamin E deficiency in different species.

In young cattle and lambs a deficiency of this vitamin is associated with the condition commonly known as muscular dystrophy. The condition is common in the United Kingdom in suckler herds in which the cows have been wintered on turnips and straw, and is most frequently seen in calves up to 3 months of age, though older animals may also show symptoms. Where the heart muscle is affected, death may be sudden without premonitory signs. Less severe cases may show symptoms of circulatory and respiratory embarrassment on the slightest exertion. Where the skeletal muscles are affected, stiffness, unnatural postures and conformation abnormalities occur. A deficiency of vitamin E may also be induced in calves by the ingestion of diets rich in unsaturated fatty acids, such as those containing excessive amounts of cod liver oil.

Since the quantity of vitamin E present in the tissue of the newborn calf and in the mother's milk is influenced by the mother's diet, it follows that pregnant animals should be given diets containing adequate amounts of the vitamin

Abnormalities in pigs caused by a vitamin E deficiency are varied, affected pigs show muscular weakness and severe liver damage, and it

TABLE 5.2 Some Conditions Associated with Vitamin E Deficiency

<i>Condition</i>	<i>Animal</i>	<i>Tissue affected</i>
1 <i>Reproductive failure</i> Embryonic degeneration Sterility	Hen, ewe, female rat Cock, male rat	Vascular system Male gonads
2 <i>Muscle degeneration</i> Muscular dystrophy Stiff lamb disease White muscle disease Fatal syncope	Chick Lamb Calf, sheep, lamb Pig, calf	Skeletal muscle Skeletal muscle Skeletal muscle + heart muscle Heart muscle
3 <i>Necrotic liver degeneration</i>	Rat, pig	Liver
4 <i>Cerebellar degeneration</i> Encephalomalacia	Chick	Cerebellum
5 <i>Exudative diathesis</i>	Rat, chick	Capillary walls
6 <i>Blood protein destruction</i>	Chick	Blood
7 <i>Body lipid degeneration</i>	Pig, chick	Depot fat oxidative rancidity <i>in vivo</i>

has been claimed that sows show low fertility 'Fatal syncope' is a vitamin E deficiency condition occurring in pigs and calves in which the heart muscle is affected and sudden death may occur

Nutritional encephalomalacia or 'crazy chick disease' may also occur in chicks on vitamin E deficient diets This is a condition in which the chick is unable to walk or stand, and is accompanied by haemorrhages and necrosis of the brain In preventing nutritional encephalomalacia vitamin E appears to function as a biological antioxidant, since the condition can be completely prevented in chicks on vitamin E deficient diets by adding either synthetic antioxidants or vitamin E

Vitamin E and Selenium

It has recently been shown that most enzootic muscular dystrophies (myopathies) in sheep and cattle can be prevented by administering

either trace amounts of selenium or vitamin E. Similarly, dietary necrotic liver degeneration in the rat and exudative diathesis in the chick can be prevented by administering either substance. Selenium, however, is ineffective in preventing nutritional encephalomalacia in the chick or muscular dystrophy induced in farm animals by dietary fats rich in unsaturated fatty acids.

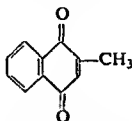
The exact interrelationship between the vitamin and selenium is not known, but it is clear that the element is not concerned with all the functions of vitamin E. Selenium itself is a very toxic element and it is unwise to use it routinely as a dietary additive. The toxic nature of selenium is discussed in the next chapter.

VITAMIN K

Vitamin K was originally discovered in 1935 to be an essential factor in the prevention of haemorrhagic symptoms produced in chicks. The discovery was made by a group of Danish scientists who gave the name 'Koagulation Factor' to the vitamin, which became shortened to the K factor and eventually to vitamin K.

Chemical Nature

A number of compounds are known to have vitamin K activity. The most important naturally occurring compound is vitamin K₁ (phyloquinone), which is chemically 2-methyl-3-phytyl-1,4-naphthoquinone. A naturally occurring naphthoquinone compound of slightly different structure is designated vitamin K₂. A number of synthetic compounds possessing vitamin K activity have been produced, and one of these, menadione or menaphthone (2-methyl-1,4-naphthoquinone), is known to be about 3.3 times as potent, biologically, as the naturally occurring vitamin K₁. It is thought that the relative effectiveness of the different vitamins K is related to their capacity for conversion into menadione in the animal body. The chemical structure of menadione is shown below:



Menadione
(2-methyl-1,4-naphthoquinone)

Vitamins K_1 and K_2 are insoluble in water but are soluble in fats. Menadione however is slightly soluble in water, and this property may have an important application in controlling its absorption from the digestive tract. Vitamins K are relatively stable at ordinary temperatures but are rapidly destroyed on exposure to sunlight.

Sources

Vitamin K_1 is present in most green leafy materials, lucerne, cabbage and kale being good sources. The amounts present in foods of animal origin are usually related to the diet, but egg yolk and fish meal are generally good sources. Vitamin K_2 is synthesised by bacteria and was originally isolated from putrefied fish meal.

Metabolism

The exact function of vitamin K in metabolism is unknown, although it has been postulated that it has a role in electron transport and oxidative phosphorylation. The vitamin is certainly necessary for the formation of prothrombin, important in the blood-clotting process.

Deficiency Symptoms

Symptoms of vitamin K deficiency have not been reported in ruminants or pigs under normal conditions, and it is generally considered that bacterial synthesis in the digestive tract supplies sufficient vitamin for the animal's needs. A number of micro organisms are known to synthesise vitamin K, including *Escherichia coli*. A disease of cattle called 'sweet clover disease' is associated with vitamin K in that spoiled sweet clover (*Melilotus albus*) contains a compound, dicoumarol, which lowers the prothrombin content of the blood. The disease can be overcome by administering vitamin K to the animals. For this reason dicoumarol is sometimes referred to as an 'anti-vitamin'.

The symptom of vitamin K deficiency in chicks is a delayed clotting time of the blood, birds are easily injured and may bleed to death. Although chicks may show these haemorrhagic symptoms, mature birds do not. The main source of vitamin K among poultry foods is green food, and 2.5 per cent dried grass in a breeder's diet permits a marginal carry-over to the chicks.

VITAMIN B COMPLEX

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The vitamins included under this heading all have the property of being soluble in water, and most of them are components of enzyme

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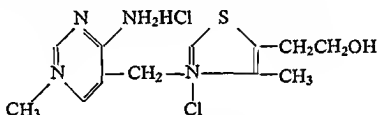
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systems Except for nicotinamide, an exogenous source of these vitamins is required, although microbial synthesis in the digestive tract can supply part of the requirements of monogastric animals, and under normal conditions the total requirements of ruminants. Deficiency symptoms do occur in pigs and poultry, but in practice it is difficult to isolate a particular vitamin as being the cause of a deficiency condition, as many of the symptoms produced are not specific and the troubles are frequently of multiple origin (Plate I) All these vitamins are available commercially

THIAMINE

Chemical Nature

Thiamine (aneurine, vitamin B₁) is a complex nitrogenous base containing a pyrimidine ring joined to a thiazole ring



Thiamine chloride hydrochloride

Because of the presence of a hydroxyl group at the end of the side-chain, thiamine can form esters. The main ester is thiamine pyrophosphate, also known as cocarboxylase. The vitamin is very soluble in water, and has a characteristic odour and 'meaty' flavour. It is fairly stable in mildly acidic solution but readily decomposes in neutral solutions.

Sources

Thiamine is widely distributed in foods. Brewers' yeast is a rich source. The vitamin is concentrated in the germ of cereal grain and is also present in the aleurone layer. Other good sources include beans, peas and green leafy crops. Animal products rich in thiamine include egg yolk, liver, kidney and pork muscle. The synthetic vitamin is obtainable and is usually marketed as the hydrochloride.

Metabolism

Thiamine pyrophosphate is a coenzyme which is involved in the oxidative decarboxylation of pyruvic acid. When the vitamin is deficient there is an accumulation of pyruvic acid and of its reduction product, lactic acid, in the tissues.

Deficiency Symptoms

Early symptoms of thiamine deficiency in most species include loss of appetite, emaciation, muscular weakness and a progressive dysfunction of the nervous system. Nerve cells are particularly dependent upon the utilisation of carbohydrates, and for this reason thiamine deficiency is more serious in nerve tissues. In pigs, appetite and growth are adversely affected, and the animals may vomit and have respiratory troubles.

Chicks reared on thiamine deficient diets have poor appetites and are consequently emaciated. After about ten days they develop polyneuritis, which is characterised by nerve degeneration and paralysis.

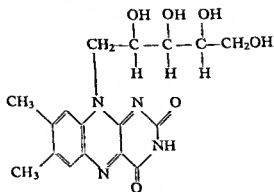
Because thiamine is fairly widely distributed in foods, and in particular because cereal grains are rich sources of the vitamin, pigs and poultry are in practice unlikely to suffer from thiamine deficiency.

Since microbial synthesis occurs in ruminants and in horses these species are unlikely to show thiamine deficiency, although symptoms have been reported in horses that have eaten *Pteridium aquilina*, a bracken which contains a thiamine antagonist (thiaminase). Raw fish also contains thiaminase, which destroys the thiamine of foods with which the fish is mixed. The activity of the thiaminase, however, is destroyed by cooking.

RIBOFLAVIN (RIBITYLFLAVINE VITAMIN B₂)

Chemical Nature

Riboflavin consists of a dimethyl isoalloxazine nucleus combined with ribose. It has the following structure:



Riboflavin



PLATE I Young pig showing symptoms of multiple vitamin deficiency (p 61)



PLATE II Effect of riboflavin deficiency in the chick's diet (p 63) Note the curled toe paralysis and the typical sitting posture



PLATE III Clubbed down in a 19 day old chick embryo, resulting from a deficiency of riboflavin in the diet of the breeding hen (p 63)



PLATE IV Effect of pantothenic acid deficiency in the chick's diet (p 66)
Lesions appear first round the eyes and at the corners of the mouth

It is a yellow, crystalline compound, which has a yellowish-green fluorescence in aqueous solution. Riboflavin is only sparingly soluble in water; it is heat-stable in acid or neutral solutions, but is destroyed by alkali. It is unstable to light, particularly ultra-violet light.

Sources

Riboflavin is widely distributed in foods, although cereal grains are poor sources. Rich sources are yeast, liver, milk (especially whey) and green leafy crops.

Metabolism

Riboflavin is an important constituent of the flavoproteins (yellow enzymes). The prosthetic group of these compound proteins contains riboflavin in the form of the phosphate (flavin mononucleotide or FMN) or in a more complex form as flavin adenine dinucleotide (FAD). There are at least ten flavoproteins which function in the animal body; they are all concerned with chemical reactions involving the transport of hydrogen. Their importance in carbohydrate metabolism is discussed in Chapter 9.

Deficiency Symptoms

In pigs, deficiency symptoms include poor appetite with consequent retardation in growth, vomiting, skin eruptions and eye abnormalities. Chicks reared on a riboflavin-deficient diet grow slowly and develop 'curled toe paralysis', a specific symptom, caused by peripheral nerve degeneration, in which the chicks walk on their hocks with the toes curled inwards (Plate II). In breeding hens, a deficiency results in decreased hatchability. Embryonic abnormalities occur, including the characteristic 'clubbed down' condition in which the down feather continues to grow inside the follicle, resulting in a coiled feather (Plate III).

Since cereals are poor sources of riboflavin but generally form the major part of the diet of pigs and poultry, deficiency troubles may occur in practice. In poultry the requirement decreases with age and chicks may recover from symptoms even though the diet is not altered. Because of bacterial action, poultry droppings are frequently richer in riboflavin than the diet. This is of great significance with floor brooding where chicks have access to the droppings.

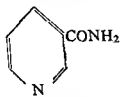
NICOTINAMIDE

Chemical Nature

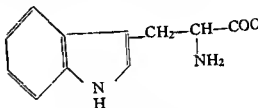
Nicotinamide is the amide derivative of nicotinic acid (niacin). The acid itself is frequently described as the vitamin, but it has been established that the compound functioning in the body is not nicotinic acid but the amide. The relationship between the two and the amino acid tryptophan, which can act as a precursor, is shown below.



Nicotinic acid



Nicotinamide



Tryptophan

Nicotinamide is a stable vitamin and is not easily destroyed by heat, acids, alkalis or by oxidation.

Sources

Nicotinic acid can be synthesised from tryptophan in the body tissues, and since animals can convert the acid to the amide, it follows that if the diet is adequately supplied with proteins rich in tryptophan, then the dietary requirement for the vitamin itself should be low or even nil. Rich sources of nicotinic acid and the amide derivative are yeast, liver and sunflower meal. Although cereal grains contain the vitamin, much of it is present in a bound form which is not readily available to pigs and poultry.

Metabolism

Nicotinamide functions in the animal body as the active group of two important coenzymes: nicotinamide adenine dinucleotide (NAD) and nicotinamide adenine dinucleotide phosphate (NADP). These coenzymes, originally known as diphospho pyridine nucleotide (DPN) and triphospho pyridine nucleotide (TPN), are involved in the mechanism of hydrogen transfer in living cells (see Chapter 9).

Deficiency Symptoms

In pigs, deficiency symptoms include poor growth, enteritis and dermatitis. In fowls a deficiency of the vitamin causes 'black tongue'.

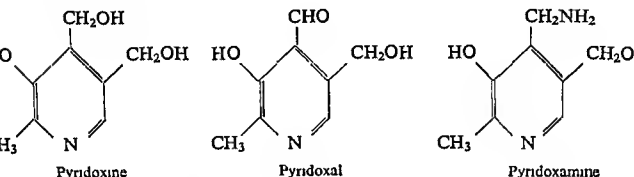
characterised by inflammation of the mouth cavity and the upper part of the oesophagus.

Most diets contain adequate amounts of nicotinamide or its precursor, tryptophan. Deficiency symptoms are likely in pigs and poultry where diets with a high maize content are used, since maize contains very little of the vitamin or of tryptophan.

VITAMIN B₆

Chemical Nature

The vitamin exists in three forms which are interconvertible in the body tissues. The parent substance is known as pyridoxine, the corresponding aldehyde derivative as pyridoxal and the amine as pyridoxamine. The term vitamin B₆ is frequently used to describe the three forms.



The amine and aldehyde derivatives are less stable than pyridoxine and are destroyed by heat.

Sources

The vitamin is widely distributed, and yeast, liver, milk, pulses and cereal grains are rich sources.

Metabolism

Of the three related compounds, the actively functioning one appears to be pyridoxal, in the form of the phosphate. Pyridoxal phosphate serves as a coenzyme involved in a number of reactions, including the decarboxylation of amino acids and transaminating mechanisms.

Deficiency Symptoms

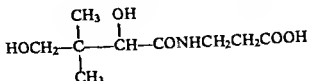
In pigs, a deficiency adversely affects the appetite and growth rate and may result in anaemia and convulsions. Chicks on a deficient diet grow very slowly and their movements are jerky, convulsions may

occur In adult birds hatchability and egg production are reduced In practice, vitamin B₆ deficiency is unlikely to occur in farm animals because of its fairly wide distribution

PANTOTHENIC ACID

Chemical Nature

Pantothenic acid is a dipeptide derivative and has the following formula



Pantothenic acid

The two components of pantothenic acid are dihydroxy dimethyl butyric acid and the amino acid, β alanine

Sources

The vitamin is widely distributed, indeed the name is derived from the Greek *pantothen*, 'from everywhere', indicating its ubiquitous distribution Rich sources are liver, egg yolk, groundnuts, peas, yeast and molasses Cereal grains are also good sources of the vitamin

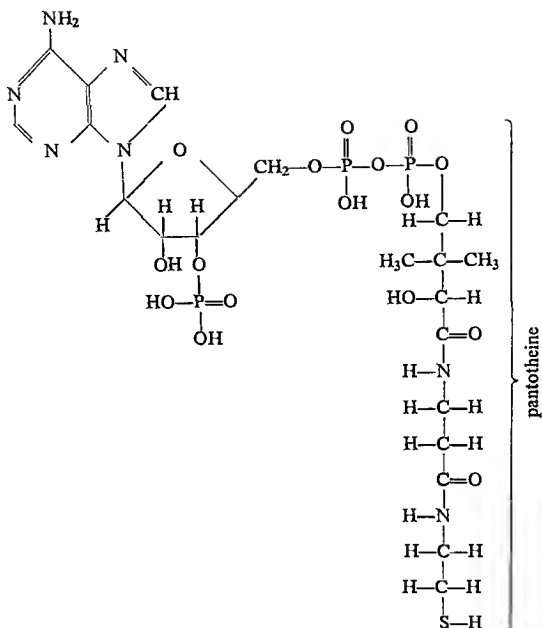
Metabolism

Pantothenic acid is a constituent of coenzyme A which is the important coenzyme of acyl transfer Chemically, coenzyme A is 3 phospho adenosine 5 diphospho pantotheine (on facing page)

The importance of coenzyme A in metabolism is discussed in Chapter 9

Deficiency Symptoms

Deficiency of pantothenic acid in pigs causes slow growth, diarrhoea, loss of hair, scaliness of the skin and a characteristic 'goose stepping' gait, in severe cases animals are unable to stand In the chick, growth is retarded and dermatitis occurs (Plate IV) In mature birds, hatchability is reduced Pantothenic acid, like all the B-complex vitamins, can be synthesised by rumen micro organisms, *Eschericia coli* for example is known to produce this vitamin Pantothenic acid deficiencies are considered to be rare in practice because of the wide distribution of



Coenzyme A

the vitamin, although deficiency symptoms have recently been reported in commercial Landrace pig herds.

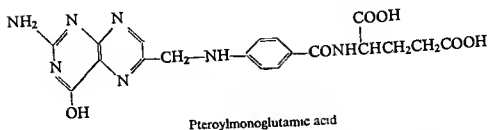
FOLIC ACID

Chemical Nature

Some confusion has arisen in naming this vitamin, since at least three associated compounds have vitamin activity. It has recently been suggested that the term 'folic acid' be retained as a group name to describe the pteroylglutamates, and that the vitamin originally known as folic acid should be renamed 'pteroylmonoglutamic acid'.

The other two compounds possessing vitamin activity are pteroyl-triglutamic acid and pteroylheptaglutamic acid, which contain three and seven glutamic acid residues respectively

The formula for pteroylmonoglutamic acid is as follows



This vitamin contains *p* aminobenzoic acid as a structural component. This compound was originally classed as a separate vitamin but is now known to be only a precursor of the pteroylglutamates

Sources

Folic acid is widely distributed in foods and is particularly abundant in green leafy foods, liver and yeast. Cereals and soya bean are also good sources.

Metabolism

Folic acid is concerned with enzyme systems controlling the transfer of hydroxymethyl groups and formyl residues. The formate unit is used in the biosynthesis of purines, serine and glycine.

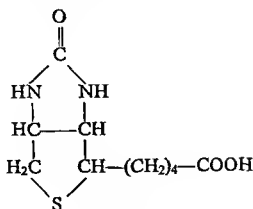
Deficiency Symptoms

A deficiency of folic acid in animals is characterised by nutritional anaemia and poor growth. With the exception of young chicks, folic acid deficiency symptoms rarely occur in farm animals because of synthesis by intestinal bacteria. Prolonged oral administration of sulphadiazine is known to depress bacterial synthesis of folic acid and deficiency symptoms may be induced by medication of this kind. Recently it has been shown that folic acid is produced in germ-free rats, which suggests that it can be formed in the animal body.

BIOTIN

Chemical Nature

Biotin has the following chemical structure



Biotin

Sources

Biotin is widely distributed in foods, liver, yeast, milk, cereals and vegetables are rich sources

Metabolism

The exact metabolic function of this vitamin in the animal is not fully understood, but it is known to have a role in fat synthesis. It has been recognised for some time to be a growth factor for yeasts and some other micro-organisms, and is thought to play a part in carbon dioxide fixation. It is suggested that biotin is a component of an energy-rich ADP-biotin enzyme complex important in carboxylation reactions. Egg white is known to contain a protein, avidin, which inactivates biotin and can lead to deficiency symptoms. The condition has been described as 'egg white injury'.

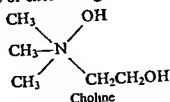
Deficiency Symptoms

Deficiency symptoms have been produced in chicks and pigs by giving experimental diets containing raw egg white or sulphur drugs. Symptoms include dermatitis and loss in weight (Plate V, facing p. 92). Since biotin is synthesised in the alimentary tract by micro-organisms, there is seldom a need for a dietary source.

CHOLINE

There is considerable doubt whether choline should be classed as a vitamin, since it can be replaced in the diet by other compounds such as methionine and betaine. Furthermore choline is present in most foods in amounts many times greater than any of the other vitamins.

The chemical structure of choline is given below



Choline is a fairly stable vitamin under normal storage conditions. It is a component of lecithins, and natural fats are generally good sources of these phospholipids (see Chapter 3). Green leafy materials, liver, yeast and cereals are rich sources.

Choline contains three labile methyl groups which can be passed on to other organic compounds. Betaine also has three labile methyl groups, while methionine has only one. This process of transmethylation is very important in many metabolic reactions. The derivative of choline, acetylcholine, is important in the transmission of nerve impulses.

Deficiency Symptoms

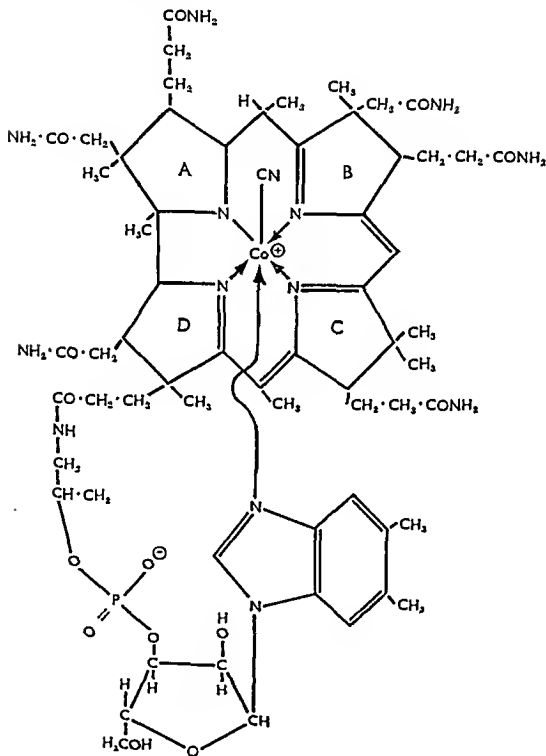
Deficiency symptoms, including slow growth and fatty infiltration of the liver, have been produced in chicks and pigs. Choline is also concerned with the prevention of perosis or slipped tendon in chicks. The choline requirement of animals is unusually large for a vitamin, but in spite of this, deficiency symptoms are not common in farm animals because of its wide distribution.

VITAMIN B₁₂

It has been known since 1926 that pernicious anaemia in man can be alleviated by feeding with raw liver. The substance in liver responsible for this was referred to as the 'anti pernicious anaemia factor' or APA. It was also well known that chicks required animal protein in their diets in order to maintain adequate growth. The term 'animal protein factor' (APF) was used to describe this substance, which occurred only in foods of animal origin. In 1948 the isolation of the APA factor was reported and it was given the name vitamin B₁₂. Trials with chicks showed that B₁₂ was also important as a constituent of APF. It was later shown, however, that vitamin B₁₂ was not the only factor concerned in the prevention of pernicious anaemia. In patients suffering from this condition the absorption of B₁₂ from the gastro-intestinal tract is impaired owing to the absence of an 'intrinsic factor' normally secreted in the gastric juice. It is believed that, although B₁₂ is the main component of APA and APF, other unknown constituents are also present in them.

Chemical Nature

Several forms of the vitamin are known. The name vitamin B₁₂ (or cyanocobalamin) is restricted to the cyanide derivative, and the structure is shown below:

Vitamin B₁₂

The most interesting feature of this structure is the presence of cobalt. The cyanide ion may be replaced by a variety of anions, e.g. hydroxyl (hydroxycobalamin or B_{12b}) or nitrite (nitritocobalamin or B_{12c}). A coenzyme containing the vitamin, named cobamide coenzyme, has been isolated, and in this a molecule of 5'-deoxyadenosine is attached to the cobalt in place of the cyanide ion. The cobamide coenzyme is unstable in the presence of light and also in the presence of anions, particularly cyanide. Under these conditions the 5'-deoxyadenosine molecule is replaced by the anion.

Sources

Vitamin B₁₂ is synthesised almost exclusively by micro-organisms and its presence in foods is thought to be ultimately of microbial origin. The main natural sources of the vitamin are foods of animal origin, liver being a particularly rich source. Its occurrence in higher plants is still controversial, since many think that its presence in trace amounts may result from contamination with bacteria or insect remains.

Metabolism

Cobamide coenzymes are important in many metabolic reactions. Of great significance in ruminant animals is the cobamide coenzyme important in the transformation of methylmalonyl coenzyme A to succinyl coenzyme A in propionic acid metabolism (see Chapter 9). A cobamide coenzyme is also important in the methylation of homocysteine to form methionine.

Deficiency Symptoms

Deficiency symptoms in farm animals generally manifest themselves as depressed growth rates. In hens a deficiency causes poor hatchability. Vitamin B₁₂ is required by ruminants, but a dietary source is not essential provided cobalt is present in the food, since microbial synthesis in the rumen provides adequate amounts (see Chapter 6).

Intestinal synthesis occurs in pigs and poultry. Organisms have been isolated from poultry excreta which synthesise vitamin B₁₂, and this has an important practical bearing on poultry housed on the deep or built up litter system, where part, if not all, of the vitamin requirements can be obtained from the litter.

It is frequently stated that vitamin B₁₂ is a dietary essential for pigs reared indoors on all plant diets. Results of feeding experiments however have been variable, and it seems likely that growth response to

B₁₂ supplementation of vegetable diets depends on the rate of intestinal synthesis, the storage level of the vitamin and the protein content of the diet.

OTHER GROWTH FACTORS INCLUDED IN THE VITAMIN B COMPLEX

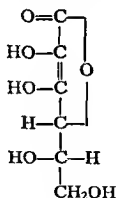
A number of other chemical substances of an organic nature have been included in the vitamin B complex. These include inositol, orotic acid and pangamic acid, but it is doubtful if these compounds have much practical significance in the nutrition of farm animals.

Other factors which appear to be of some significance in poultry nutrition are the grass factor, whey factor and fish factor. The evidence for these has been obtained from growth responses in feeding trials and from hatchability studies.

VITAMIN C

Chemical Nature

Vitamin C is chemically known as L-ascorbic acid and has the following formula:



L-ascorbic acid

The vitamin is a colourless, crystalline, water-soluble compound having acidic and strong reducing properties. It is heat-stable in acid solution but is readily decomposed in the presence of alkali. The destruction of the vitamin is accelerated by exposure to light.

Sources

Well-known sources of this vitamin are citrus fruits and green leafy vegetables. Synthetic ascorbic acid is available commercially.

Metabolism

Ascorbic acid and its oxidation product, dehydroascorbic acid, play an important part in various oxidation-reduction mechanisms in living cells. With the exception of the primates and the guinea-pig, all animals can synthesise ascorbic acid from the D glucuronic acid present in their tissues.

Deficiency Symptoms

Farm animals do not require a dietary source of this vitamin and deficiency symptoms are therefore unknown.

HYPERVITAMINOSIS

Hypervitaminosis is the name given to pathological conditions resulting from an overdose of vitamins. Under natural conditions it is unlikely that farm animals will receive excessive doses of vitamins, although where synthetic vitamins are added to diets there is always the risk that abnormally large amounts may be ingested if errors are made during mixing. There is experimental evidence that toxic symptoms can occur if animals are given excessive quantities of vitamin A or D. Most of these experiments have been carried out with rats, in which symptoms of hypervitaminosis A include impaired growth, emaciation, anaemia and bone fractures. Excessive intakes of vitamin D cause abnormally high levels of calcium and phosphorus in the blood, resulting in the deposition of calcium salts in the arteries and organs. Symptoms of hypervitaminosis D₃ have been noted in cattle and calves.

Depression in growth and anaemia due to excessive doses of menadione (synthetic vitamin K) have been reported.

FURTHER READING

- L. J. HARRIS, 1955 *Vitamins in Theory and Practice* Cambridge University Press
- W. H. SEBRELL AND R. S. HARRIS (ed.) 1954 *The Vitamins* Academic Press New York and London
- M. L. SCOTT, 1962. Anti oxidants, selenium and sulphur amino acids in the vitamin E nutrition of chicks. A review article *Nutrition Abstracts and Reviews* 32, 18
- R. S. HARRIS and D. J. INGLE (ed.) *Vitamins and Hormones: Advances in Research and Applications* (Annual vols since 1942) Academic Press, New York and London

MINERALS

It is known that there are about 40 mineral elements which occur regularly in animal tissues. Many of these however are thought to be present merely because they are constituents of the animal's food, and certainly some of them do not appear to serve any essential function in the animal's metabolism. The term 'essential mineral elements' is therefore restricted to those mineral elements which have been proved to have a metabolic role in the body. Before an element can be classed as essential it is generally considered necessary to prove that purified diets lacking the element cause deficiency symptoms in animals, and that these symptoms can be cured or prevented by adding the element to the experimental diet. Most research on mineral nutrition has been carried out in this way, but unfortunately some of the mineral elements required by animals for normal health and growth are needed in such minute amounts that the construction of purified diets is often difficult to achieve. Fifteen mineral elements are known to be essential, and there is some evidence, though it is not conclusive, that four other elements may also be essential.

The mineral elements are usually divided into two groups according to the concentration present in the animal body. These groups are termed major or macro-elements and trace or micro-elements. The essential mineral elements and their approximate amounts in the animal body are given in Table 6.1. The trace elements are present in the animal body in a concentration not greater than 1 part in 20,000; because of this low concentration the quantities present in animal or plant tissues are frequently expressed in terms of parts per million (ppm) rather than as percentages.

The study of animal mineral nutrition is a complex one, and although it is convenient to discuss each element individually, many function in the body in pairs or groups.

Some minerals occur as structural components, and a number act as enzyme activators. Many elements, such as iron and potassium, are known to occur in every cell in the animal body and clearly play a fundamental role in cell metabolism. Some elements, notably calcium and molybdenum, may interfere with the absorption and activity of

other elements. This interaction of minerals with each other is an important factor in animal nutrition, and an imbalance of mineral elements—as distinct from a simple deficiency—is important in the aetiology of certain nutritional disorders of farm animals. The use of radioactive isotopes in recent years has advanced our knowledge of mineral nutrition, although there are many nutritional diseases associated with minerals whose exact cause is still unknown.

TABLE 6.1 Essential Mineral Elements and their Approximate Concentrations in the Animal Body

<i>Essential Elements</i>				<i>Probably Essential Elements</i>
<i>Major</i>	<i>Per cent</i>	<i>Trace</i>	<i>ppm</i>	<i>Trace</i>
Calcium	1.5	Iron	20-80	Fluorine
Phosphorus	1.0	Zinc	10-50	Bromine
Potassium	0.2	Copper	1.5	Barium
Sodium	0.16	Manganese	0.2-0.5	Strontium
Chlorine	0.11	Iodine	0.3-0.6	
Sulphur	0.15	Cobalt	0.02-0.1	
Magnesium	0.04	Molybdenum	1-4	
		Selenium	—	

Many of the essential elements can also be classed as 'toxic minerals', since if they are given to the animal in excess they can be harmful and even fatal. This is particularly true of copper, selenium, molybdenum and fluorine. Copper and fluorine are cumulative poisons, since the animal body is unable to excrete them efficiently, small amounts of these elements given in excess of the animal's daily needs will in time produce toxic symptoms. Supplementation of any diet with minerals should always be carried out with great care and the indiscriminate use of trace elements in particular be avoided.

MAJOR ELEMENTS

CALCIUM

Calcium is the most abundant mineral element in the animal body. It is an important constituent of the skeleton and teeth, in which about 99 per cent of the total body calcium is found, and in addition it is an essential constituent of most living cells and tissue fluids. It functions in the regulation of the excitability of the nervous system, it is necessary for the normal action of skeletal and heart muscle, and it is concerned in the coagulation of blood. In blood the element occurs in the

plasma, none being present in the cells. The plasma of animals usually contains from 8 to 12 mg calcium per 100 ml, although that of laying hens contains more.

Composition of bone. Bone is highly complex in structure, the dry matter consisting of approximately 46 per cent. mineral matter, 36 per cent. protein and 18 per cent. fat. The composition varies, however, according to the age and nutritional status of the animal. Calcium and phosphorus are the two most abundant mineral elements in bone; they are combined in a form similar to that found in the mineral fluorapatite ($3\text{Ca}_3(\text{PO}_4)_2 \cdot \text{CaF}_2$). The fluorine may be replaced by an OH or CO_3 radical in bone. Bone ash contains approximately 36 per cent. calcium, 17 per cent. phosphorus and 1 per cent. magnesium.

The skeleton is not a stable unit in the chemical sense, since large amounts of the calcium and phosphorus in bone can be liberated by resorption. This takes place particularly during lactation and egg production, although the exchange of calcium and phosphorus between bones and soft tissue is always a continuous process. This resorption of calcium is controlled by the action of the parathyroid gland. If animals are fed on a low calcium diet, the parathyroid gland is stimulated and the hormone produced causes resorption of bone, liberating calcium to meet the requirements of the animal. Since calcium is combined with phosphorus in bone, the phosphorus is also liberated and excreted by the animal.

Deficiency Symptoms

If calcium is deficient in the diet of young growing animals, then adequate bone formation cannot occur and the condition known as rickets is produced. The symptoms of rickets are misshapen bones, enlargement of the joints, lameness and stiffness. In adult animals calcium deficiency produces osteomalacia, in which the calcium in the bone is withdrawn and not replaced. In osteomalacia the bones become weak and are easily broken. In hens, deficiency symptoms are soft beak and bones, retarded growth and bowed legs; the eggs have thin shells and egg production may be reduced. The symptoms described above for rickets and osteomalacia are not specific for calcium and can also be produced by a deficiency of phosphorus, or an abnormal calcium:phosphorus ratio, or a deficiency of vitamin D. It is obvious that a number of factors can be responsible for subnormal calcification.

Milk fever (parturient paresis) is a condition which most commonly occurs in dairy cows shortly after calving. It is characterised by a lowering of the serum calcium level, muscular spasms, and in extreme

cases paralysis and unconsciousness. It is suggested that the low blood calcium level (hypocalcaemia) may be caused by the parathyroid glands being unable to mobilise sufficient calcium to meet the high requirements of the animal for milk production. Normal levels of blood calcium can be restored by intravenous injections of calcium gluconate, but this may not always have a permanent effect.

Sources of Calcium

Milk and green leafy crops, especially legumes, are good sources of calcium, cereals and roots are poor sources. Animal by products containing bone, such as fish meal, and meat and bone meal, are excellent sources. Mineral supplements which are frequently given to farm animals, especially lactating animals and laying hens, include ground limestone, steamed bone flour and dicalcium phosphate. If rock calcium phosphate is given to animals it is important to ensure that fluorine is absent, as otherwise this supplement may be toxic.

Calcium Phosphorus Ratio

In giving calcium supplements to animals it is important to consider the calcium phosphorus ratio of the diet since an abnormal ratio may be as harmful as a deficiency of either element in the diet. The calcium phosphorus ratio considered most suitable for farm animals other than poultry is generally within the range 1:1 to 2:1. The proportion of calcium for laying hens is much larger, since they require great amounts of this element for eggshell production. The calcium is usually given to laying hens as ground limestone mixed with the diet, or alternatively calcareous grit may be given *ad lib*.

PHOSPHORUS

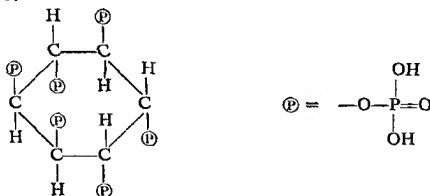
Phosphorus is closely associated with calcium in the animal body. In addition to its presence in bone it occurs in phosphoproteins, nucleic acids and phospholipids. The element plays an important part in carbohydrate metabolism in the formation of hexose phosphates and adenosine di and tri phosphates. The phosphorus content of the animal body is rather smaller than the calcium content. Whereas 99 per cent. of the calcium found in the body occurs in the bones and teeth, the proportion of the phosphorus in these structures is about 80 per cent. of the total. The amount of phosphorus present in blood serum is usually within the range 4 to 12 mg per 100 ml.

Deficiency Symptoms

Since phosphorus is required for bone formation, a deficiency can cause rickets or osteomalacia. 'Pica' or depraved appetite has been noted in cattle when there is a deficiency of phosphorus in their diet; the affected animals have abnormal appetites and chew wood, bones, rags and other foreign materials. Pica is not specifically a sign of phosphorus deficiency since it may be caused by other factors. Evidence of phosphorus deficiency may be obtained from an analysis of blood serum, which would show a phosphorus content lower than normal. In chronic phosphorus deficiency animals may have stiff joints and muscular weakness. Low dietary intakes of phosphorus have also been associated with low fertility and low milk yield in cows and with stunted growth in young animals. Phosphorus deficiency is usually more common in cattle than in sheep, as the latter tend to have more selective grazing habits and choose the growing parts of plants which happen to be richer in phosphorus.

Sources of Phosphorus

Milk, cereal grains, fish meal and meat products containing bone are good sources of phosphorus; the content in hays and straws is generally very low. Considerable attention has been paid to the availability of phosphorus. Much of the element present in cereal grains is in the form of phytates, which are salts of phytic acid, a phosphoric acid derivative:



Phytic acid

Insoluble calcium and magnesium phytates occur in cereals and other plant products. Experiments with chicks have shown that the phosphorus of calcium phytate is utilised only 10 per cent. as effectively as disodium phosphate. In studies with laying hens, phytate phosphorus was utilised about half as well as dicalcium phosphate. In pigs some of the phytate phosphorus is made available in the stomach by the

action of plant phytase enzymes present in the food. It has also been shown with sheep that hydrolysis of phytates by bacterial phytases occurs in the rumen. Phytate phosphorus appears therefore to be utilised by ruminants as readily as other forms of phosphorus, although studies using radioactive isotopes indicate that the availability of phytate phosphorus may range from 33 to 90 per cent.

POTASSIUM

Potassium plays a very important part, along with sodium, chlorine and bicarbonate ions, in the osmotic regulation of the body fluids. Whereas sodium is the main inorganic cation of extracellular tissue fluids, potassium functions principally as the cation of cells. Potassium plays an important part in nerve and muscle excitability, and is also concerned in carbohydrate metabolism.

Deficiency Symptoms

The potassium content of plants is generally very high, the amount present in grass dry matter, for example, being frequently above 2.5 per cent, so that it is normally ingested by animals in larger amounts than any other element. Consequently it is extremely unlikely that potassium deficiency could occur in farm animals under natural conditions. No cases have ever been reported under farming conditions, although deficiency symptoms have been produced in chicks fed on experimental diets low in this mineral. Symptoms in chicks included retarded growth, weakness and tetany, followed by death. Deficiency symptoms, including severe paralysis, have also been recorded for calves fed on synthetic milk diets low in potassium.

A dietary excess of potassium is normally rapidly excreted from the body, chiefly in the urine. Some workers believe that high intakes of the element may interfere with the absorption and metabolism of magnesium in the animal, which may be an important factor in the aetiology of hypomagnesaemic tetany.

SODIUM

Most of the sodium of the animal body is present in the soft tissues and body fluids. Like potassium, sodium is concerned with the acid-base balance and osmotic regulation of the body fluids.

Sodium is the chief cation of blood plasma and other extra cellular fluids of the body. The sodium concentration within the cells is

relatively low, the element being replaced largely by potassium and magnesium. Much of the sodium is ingested in the form of sodium chloride (common salt), and it is also mainly in this form that the element is excreted from the body. Many experiments have been carried out to determine the salt requirements of different animals, and there is evidence that sodium rather than chlorine is the chief limiting factor in salt-deficient diets of sheep and cows.

Deficiency Symptoms

A deficiency of sodium in the diet retards the growth of animals and reduces the utilisation of digested proteins and energy. In hens, egg production is adversely affected as well as growth. Experiments carried out on rats fed on low-sodium diets resulted in eye lesions, reproductive disturbances and finally death.

Sources of Sodium

Most foods of vegetable origin have comparatively low sodium contents; animal products, especially meat meals and foods of marine origin, are richer sources. The commonest mineral supplement given to farm animals is common salt.

CHLORINE

Chlorine is associated with sodium and potassium in acid-base relationships and osmosis. Chlorine also plays an important part in the gastric secretion, where it occurs as hydrochloric acid as well as chloride salts. Chlorine is excreted from the body in the urine and is also lost from the body, along with sodium and potassium, in perspiration. Experiments with rats on chlorine-deficient diets showed that growth was retarded, but no other symptoms developed.

Sources of Chlorine

With the exception of fish and meat meals, the chlorine content of most foods is comparatively low. The chlorine content of pasture grass varies widely and figures ranging from 0.003 per cent. to 0.342 per cent. have been reported. The main source of this element for most animals is common salt.

Common salt. Since plants tend to be low in both sodium and chlorine, it is the usual practice to give common salt to herbivores. Unless salt is available deficiencies are likely to occur in both cattle

and sheep Experiments carried out in the U S A with dairy cows on salt deficient diets showed that animals did not exhibit immediate ill effects, but eventually appetite declined, with subsequent loss in weight and lowered milk production The addition of salt to the diet produced an immediate cure

Salt is also important in the diet of hens, and it is known to counteract feather picking and cannibalism Salt is generally given to pigs on vegetable diets, but if fish meal is given the need for added salt is reduced Swill can also be a rich source of salt, although the product is very variable and can contain excessive amounts Too much salt in the diet is definitely harmful and causes excessive thirst, muscular weakness and oedema Salt poisoning is quite common in pigs and poultry, especially where fresh drinking water is limited When the concentration of salt in the diet of hens exceeds 4 per cent and the supply of drinking water is limited, then death may occur Hens can tolerate larger amounts of salt if plenty of water is available Chicks cannot tolerate salt as well as adults, and 2 per cent in the diet should be regarded as the absolute maximum Turkey poult are even less tolerant, and 1 per cent of salt in the diet should not be exceeded

SULPHUR

Most of the sulphur in the animal body occurs in proteins containing the amino acids cystine, cysteine and methionine The two vitamins, biotin and thiamine, and the hormone insulin, also contain sulphur Only a small amount of sulphur is present in the body in inorganic form, though sulphates are known to occur in the blood in small quantities Wool is rich in cystine and contains about 4 per cent of sulphur

Deficiency of this element in the body is not usually considered, since the intake is mainly in the form of protein and a deficiency of sulphur would indicate a protein deficiency However, in ruminant diets in which urea is used as a partial nitrogen replacement for protein nitrogen, sulphur may be limiting for the synthesis of cysteine, cystine and methionine Under these conditions the addition of sulphur to urea-containing rations may be beneficial, since it has been established, through the use of labelled sulphur [^{35}S], that the rumen micro organisms can utilise inorganic sulphur There is some evidence that sodium sulphate can be used by the micro organisms more efficiently than elemental sulphur

MAGNESIUM

Magnesium is closely associated with calcium and phosphorus. About 70 per cent. of the total magnesium is found in the skeleton, the remainder being distributed in the soft tissues and fluids. Magnesium is known to be an activator of phosphates, and also functions in carbohydrate metabolism (see Chapter 9).

Deficiency Symptoms

Symptoms due to a simple deficiency of magnesium in the diet have been reported for a number of animals. In rats fed on purified diets the symptoms include increased nervous irritability and convulsions. Experiments carried out on calves reared on low-magnesium milk diets resulted in low serum magnesium levels, depleted bone magnesium, tetany and death. The condition is not uncommon in milk-fed calves about 50-70 days old.

In adult ruminants a condition known as hypomagnesaemic tetany associated with low blood levels of magnesium (hypomagnesaemia) has been recognised since the early thirties. A great deal of attention has been given to this condition in recent years, since it is widespread and the death rate is high. The annual incidence of clinical cases in dairy cattle in the United Kingdom was estimated in 1960 to be about 0.5 per cent. The condition is reported to be more widespread in the Netherlands, where it has been estimated that the incidence in dairy cattle may be 1 to 2 per cent.

Hypomagnesaemic tetany has been known under a variety of names, including magnesium tetany, lactation tetany and grass staggers, but most of these terms have been discarded because the disease is not always associated with lactation nor with grazing animals. The condition can affect stall-fed dairy cattle, hill cattle, bullocks and cattle at grass as well as sheep. It is probably true to say that most cases occur in grazing animals, and the trouble is particularly common in the spring when animals are turned out on to young succulent pasture, and in the autumn when animals are grazed too long without adequate supplementary feeding. The onset of tetany may be very sudden and in many cases the animals do not recover. In adult animals the bone magnesium does not seem to be readily available to prevent hypomagnesaemia occurring.

The normal magnesium content of blood serum in cattle is within the range of 1.7 to 4 mg magnesium per 100 ml blood serum, but levels below 1.7 frequently occur without clinical symptoms of disease.

Tetany is usually preceded by a fall in blood serum magnesium to about 0.5 mg per 100 ml. Injection of magnesium sulphate can generally be expected to cure the animal if given early, but in practice this is sometimes difficult. Typical symptoms of tetany are nervousness, tremors, twitching of the facial muscles, staggering gait and convulsions.

The exact cause of hypomagnesaemic tetany in ruminant animals is unknown, although a dietary deficiency of magnesium may be a contributing factor. Some research workers consider that the condition may be caused by a cation-anion imbalance in the diet. Others suggest that excessive ruminal ammonia production may be the cause, or a hormonal upset.

More recent work using radioactive magnesium in tracer studies indicates that the magnesium present in the food is poorly absorbed from the alimentary canal, in some cases only 10-20 per cent of the herbage magnesium can be utilised by the ruminant. Why this is so in ruminants is not known. Since adult animals have only very small readily available reserves of body magnesium they are dependent upon a regular dietary supply.

Although its cause is still uncertain, a high degree of success in reducing the incidence and severity of hypomagnesaemia may be obtained by increasing the magnesium intake. This can be effected by feeding with magnesium-rich mineral mixtures, or alternatively by increasing the magnesium content of pasture by the application of magnesium fertilisers.

Sources of Magnesium

Wheat bran, dried yeast and most vegetable protein concentrates, especially cottonseed cake and linseed cake, are good sources of magnesium. Clovers are usually richer in magnesium than grasses, although the magnesium content of forage crops varies widely. The mineral supplement most frequently used is magnesium oxide, which is sold commercially as calcined magnesite. When hypomagnesaemic tetany is likely to occur it is generally considered that about 50 g of magnesium oxide should be given to cows per head per day as a prophylactic measure.

TRACE ELEMENTS

IRON

More than 90 per cent of the iron in the body is combined with proteins, the most important protein being haemoglobin, which contains

about 0.34 per cent. of the element. Iron also occurs in blood serum bound to a protein called siderophilin, believed to be concerned with the transportation of iron from one part of the body to another. Ferritin is a brown iron-containing protein containing up to 20 per cent. of the element, which is present in the spleen, liver, kidney and bone marrow; ferritin is probably the form in which iron is stored. Haemosiderin is a similar iron storage compound which may contain up to 35 per cent. of the element. Iron is also a component of many enzymes, including cytochromes and certain flavoproteins.

Deficiency Symptoms

Since more than half the iron present in the body occurs as haemoglobin, a dietary deficiency of iron would clearly be expected to affect the formation of this compound. The red blood corpuscles contain haemoglobin, and these cells are continually being produced in the bone marrow to replace those red cells destroyed in the animal body as a result of katabolism. Although the haemoglobin molecule is destroyed in the katabolism of these red blood corpuscles, the iron liberated is made use of in the resynthesis of haemoglobin, and because of this the daily requirement of iron by a healthy animal is usually small. If the need for iron increases, as it would after prolonged haemorrhage or during pregnancy, then haemoglobin synthesis may be affected and anaemia will result. Anaemia due to iron deficiency occurs most commonly in rapidly growing sucklings, since the iron content of milk is usually very low; this frequently occurs in pigs housed in pens without access to soil or pasture. The young piglet must retain about 7 mg of iron per day to grow at a normal rate without becoming anaemic; since the sow's milk only provides about 1 mg per day there is an additional requirement of about 6 mg. This should be provided by dosing or injection with iron salts. Giving additional iron to the lactating females does not prevent anaemia occurring in the young piglets, as the iron content of milk is not increased by feeding.

Iron deficiency anaemia is not common in lambs and calves because in practice it is unusual to restrict them to a milk diet without supplementary feeding. It does however sometimes occur in laying hens, since egg production represents a considerable drain on the body reserves.

Sources of Iron

Apart from milk, which is a poor source, iron is widely distributed in foods. Excellent sources of the element are green leafy materials,

most leguminous plants and seed enats It is present in foods in several forms, some of which are available to the animal and some absorbed with difficulty Blood meal, for example, contains a relatively large amount of iron but it is poorly utilised

It has long been held that the absorption of iron is to a large extent independent of the dietary source and that iron is absorbed according to need by a limiting mechanism known as the 'mucosal block' The mucosal block theory implies that excessive amounts of iron are prevented from entering the body by a regulating mechanism brought about by the mucosal cells of the gastro intestinal tract and that iron absorption is therefore largely controlled by body requirements The mucosal block theory has, however, recently been discredited by certain workers, and the problem of iron absorption is still a debatable one

The adult's need for iron is normally low, since the iron produced from the destruction of haemoglobin is made available for haemoglobin regeneration, only about 10 per cent of the element escaping from this cycle

Excess of iron in the diet may cause alimentary disturbances

COPPER

Evidence that copper is a dietary essential was obtained in 1924, when experiments with rats showed that copper was necessary for haemoglobin formation Although copper is not actually a constituent of the haemoglobin molecule it is thought to be an essential component of the mature red blood corpuscles, and a certain minimum amount of copper is necessary for the production of the red corpuscles and for maintaining their activity in the circulation Copper is known to be a component of many enzyme systems, and it also occurs in certain pigments, notably turacin, a pigment of feathers The element is necessary for the normal pigmentation of hair, fur and wool It is thought to be present in all body cells, being particularly concentrated in the liver, which acts as the main storage organ of the body for copper

Deficiency Symptoms

Since copper performs many functions in the animal body there are a variety of deficiency symptoms These include anaemia, poor growth, bone disorders, scouring depigmentation of hair and wool, gastrointestinal disturbances and lesions in the brain stem and spinal cord

The lesions are associated with muscular incoordination, and occur especially in young lambs. A copper deficiency condition known as 'enzootic ataxia' has been known for some time in Australia. The disorder is there associated with pastures low in copper content (2 to 4 ppm in the dry matter), and can be prevented by feeding with a copper salt. A similar condition which affects lambs occurs in the United Kingdom and is known as 'swayback', and although this disease can be prevented by dosing the ewe with copper sulphate during pregnancy, the trouble does not appear to be caused invariably by a simple dietary deficiency of copper. Swayback has been reported to occur on pastures apparently normal or even high (7 to 15 ppm) in copper content. In such cases the exact cause of swayback is not yet known. The symptoms of this condition in newborn lambs range from a complete inability to stand to various degrees of incoordination, particularly of the hind limbs. Older lambs which develop swayback show similar symptoms. The lesions are irreversible and the mortality rate is high.

Copper-molybdenum-sulphate Interrelations

Certain pastures on calcareous soils in parts of England have been known for over a hundred years to be associated with a condition in cattle described as 'teart', characterised by unthriftiness and scouring. A similar disorder occurs on reclaimed peat lands in New Zealand, where it is known as 'peat scours'. Molybdenum levels in teart pasture are of the order of 20 to 100 ppm compared with 3 to 5 ppm in normal pastures, and teart was originally regarded as being a straightforward molybdenosis. In the late nineteen-thirties, however, it was demonstrated that feeding with copper sulphate controlled the scouring, and hence a molybdenum-copper relationship was established. It is now known that the effect of molybdenum is complex, and it has been suggested that the element exerts its limiting effect on copper retention in the animal only in the presence of sulphate.

Cattle appear to be more vulnerable to molybdenum poisoning than sheep; horses and pigs are not usually affected when grazing teart pastures.

Sources of Copper

Copper is widely distributed in foods and under normal conditions the diet of farm animals is likely to contain adequate amounts. The copper content of crops is related to a large extent to the soil copper level, but other factors such as drainage conditions and the herbage species affect the copper content. Seeds and seed by-products are

usually rich in copper, but straws contain little. The normal copper content of pasture dry matter ranges from about 4 to 8 ppm. The copper content of milk is low, and hence it is customary when dosing young animals, especially piglets, with an iron salt to include a trace of copper sulphate.

Copper Toxicity

It has long been known that copper salts given in excess to animals are toxic. Continuous ingestion of copper in excess of nutritional requirements leads to an accumulation of the element in the body tissues, especially in the liver. Copper can be regarded as a cumulative poison, so that considerable care is required in administering copper salts to animals. It is unwise to administer copper supplements to sheep unless deficiency conditions are liable to occur—many cases of death due to copper poisoning caused by the indiscriminate use of copper fortified diets have been reported. Chronic copper poisoning in sheep has occurred under natural conditions in parts of Australia where the copper content of the pasture is high. Sheep seem to be particularly susceptible to copper poisoning.

COBALT

A number of disorders of cattle and sheep, characterised by an emaciation and listlessness typical of malnutrition, have been recognised for many years and have been described as 'pining', 'salt sick', 'bush sickness' and 'wasting disease'. A number of areas in many different parts of the world are associated with this type of disorder. There are such areas in parts of Australia, New Zealand and the U.S.A. In the United Kingdom 'pining pastures' occur in many counties and are particularly common in the border counties of England and Scotland.

As early as 1807 Hogg the Ettrick shepherd, recognised 'pining' or 'vinquish' as being a dietary upset. It is now known that pinning is associated with a dietary deficiency of cobalt caused by low concentrations of the element in the soil and pastures. Pinning can be prevented in these areas by feeding with small amounts of cobalt.

The physiological function of cobalt was only discovered when vitamin B₁₂ was isolated and was shown to contain the element. Cobalt is required by micro organisms in the rumen for the synthesis of vitamin B₁₂, and if the element is deficient in the diet then the vitamin

cannot be produced in the rumen in amounts sufficient to satisfy the animal's requirements, and symptoms of pining occur. Pining is therefore regarded as being due to a deficiency of vitamin B₁₂. There is evidence for this, since injections of vitamin B₁₂ into the blood alleviate the condition, whereas cobalt injections have little beneficial effect. Although vitamin B₁₂ therapy will prevent pining occurring in ruminant animals, it is more convenient and cheaper in cobalt-deficient areas to supplement the diet with the element, allowing the micro-organisms in the rumen to synthesise the vitamin for subsequent absorption by the host.

There is evidence that the intestinal micro-organisms in non-ruminants also can synthesise vitamin B₁₂, although in pigs and poultry this synthesis may be insufficient to meet their requirements. It is common practice to include in pig and poultry diets some animal protein food rich in vitamin B₁₂ in preference to including a cobalt salt.

Apart from the importance of cobalt as a component of vitamin B₁₂, the element is believed to have other functions in the animal body as an activating ion in certain enzyme reactions.

Sources of Cobalt

Most foods contain traces of cobalt. Normal pastures have a cobalt content in the dry matter within the range 0.1 to 0.25 ppm. Deficient pastures usually contain less than 0.08 ppm.

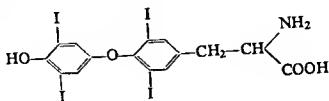
Cobalt deficiency in ruminants can be prevented by dosing the animals with cobalt sulphate, although this form of treatment has to be repeated at short intervals. A continuous supply from a single dose can be obtained by giving a cobalt bullet containing 90 per cent. cobaltic oxide; the bullet remains in the reticulum and slowly releases the element over a long period of time. Some of this cobalt is not utilised by the animal and is excreted, and this of course has the effect of improving the cobalt concentration of the pasture. Alternatively, deficient pastures can be top-dressed with small amounts of cobalt sulphate.

Cobalt Toxicity

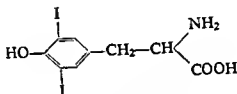
Although an excess of cobalt can be toxic to animals, there is a wide margin of safety between the nutritional requirement and the toxic level. Cobalt toxicosis is extremely unlikely to occur under practical farming conditions. Unlike copper, cobalt is poorly retained by the body tissues and an excess of the element is soon excreted. The toxic level of cobalt for cattle is 40 to 50 mg cobalt per 100 lb body weight daily.

IODINE

The amount of iodine present in the animal body is very small and in the adult is usually less than 0.6 ppm. Although the element is distributed throughout the tissues and secretions, its main role appears to be as a constituent of the hormone, thyroxine, produced by the thyroid gland.



Thyroxine



Diiodotyrosine

The element also occurs in the thyroid gland as a constituent of diiodotyrosine, which is an intermediate product in the formation of thyroxine from the amino acid, tyrosine. Both diiodotyrosine and thyroxine occur in the thyroid gland as components of the protein thyroglobulin; this compound acts as a store of thyroxine, liberating the hormone when required to perform its function of controlling the metabolic rate.

Deficiency Symptoms

When the diet contains insufficient amounts of iodine the production of thyroxine is decreased. The main indication of such a deficiency is an enlargement of the thyroid gland, termed endemic goitre. The thyroid being situated in the neck, the deficiency condition in farm animals manifests itself as a swelling of the neck, 'big neck'. Reproductive failure is one of the most outstanding consequences of reduced thyroid function; breeding animals deficient in iodine give birth to hairless, weak or dead young.

A dietary deficiency of iodine is not the sole cause of goitre; it is known that certain foods contain goitrogenic compounds and cause goitre in animals if given in large amounts. These foods include most

members of the *Brassica* family, especially kale, cabbage and rape, and also soya beans, linseed, peas and groundnuts. Goitrogens have been reported in milk of cows fed on goitrogenic plants. A goitrogen present in swede seeds has been identified as L-5-vinyl-2-thiooxalidone (goitrin). Thiocyanate, which may also be present in members of the *Brassica* family, is known to be goitrogenic and may be produced in the tissues from a cyanogenetic glycoside present in some foods. The mechanism of the action of these goitrogenic substances is not fully understood.

Goitrogenic activity of the thiocyanate type is prevented by supplying adequate iodine in the diet.

Sources of Iodine

Iodine occurs in traces in most foods. The richest sources are foods of marine origin, and values as high as 0.2 per cent iodine have been reported for some seaweeds. Fish meal is also a rich source of the element. The iodine content of land plants is related to the amount of iodine present in the soil, and consequently wide variations occur in similar crops grown in different areas.

In areas where goitre is endemic precautions are generally taken by supplementing the diet with the element, usually in the form of iodised salt. This compound contains the element either as sodium or potassium iodide or as sodium iodate.

MANGANESE

The amount of manganese present in the animal body is extremely small. Most tissues contain traces of the element, the highest concentrations occurring in the bones, liver, kidney, pancreas and pituitary gland. Manganese is important in the animal body as an activator of certain enzyme reactions concerned with carbohydrate, protein and lipid metabolism.

Deficiency Symptoms

Symptoms of manganese deficiency were first noted in rats fed on purified diets. The animals grew slowly and bone structure and reproduction were affected. The reproductive failures were quite marked and included defective ovulation in females and testicular degeneration and sterility in males.

Manganese deficiency is unlikely to occur in ruminants kept under natural conditions, although deficiency symptoms have been reported in young cattle grazing certain pastures on sand and peat soils in the

Netherlands. These symptoms included poor growth, leg deformities, poor fertility and frequent abortion. Manganese is an important element in the diet of young chicks in the prevention of perosis or 'slipped tendon', a malformation of the leg bones. It is not, however, the only factor involved in the aetiology of this condition, as perosis in young birds may be aggravated by high dietary intakes of calcium and phosphorus. Manganese deficiency in breeding birds causes reduced hatchability, reduced shell thickness, and head retraction in chicks (Plate VI, opposite). In pigs lameness is a symptom.

Sources of Manganese

The element is widely distributed in foods, and most pastures contain 40-200 ppm in the dry matter. The manganese content of pastures, however, can vary over a much wider range and in acid conditions may be as high as 500-600 ppm. Seeds and seed products contain moderate amounts, except for maize which is low in the element. Yeast and most foods of animal origin are also poor sources of manganese. Rich sources are rice bran and wheat offals. Most green foods contain adequate amounts.

Manganese Toxicity

There is a wide margin of safety between the toxic dose of manganese and the normal level in foods. Levels as high as 1000 ppm have been given to hens without evidence of toxicity.

ZINC

Zinc has been found in every tissue in the animal body. The element tends to accumulate in the bones rather than the liver, which is the main storage organ of many of the other trace elements. High concentrations have been found in the skin, hair and wool of animals. Several enzymes in the animal body are known to contain zinc, these include carbonic anhydrase, pancreatic carboxypeptidase and glutamic dehydrogenase.

Deficiency Symptoms

Zinc deficiency has been produced experimentally in rats, the symptoms including slow growth, testicular atrophy, skin lesions and interference with hair development. A deficiency of this element is unlikely to occur in grazing animals because of the relatively high amounts present in natural pastures. Recently considerable attention



PLATE V. Effect of biotin deficiency in the diet of the chick (p. 69) Lesions appear first on the feet



PLATE VI. Head retraction in a newly hatched chick; typical symptom of manganese deficiency in the breeder's diet (p. 92).

has been given to a zinc deficiency condition in pigs resulting in parakeratosis. Symptoms of this deficiency are subnormal growth, poor feed efficiency and skin lesions characterised by reddening of the skin of the belly, followed by eruptions which develop into scabs. Parakeratosis is particularly liable to occur in young intensively housed pigs fed *ad lib.* on a dry diet, though a similar diet given wet does not appear to cause the condition. It is aggravated by increased calcium levels in the diet, and decreased by reduced calcium and increased phosphorus levels. The trouble can be prevented by adding small amounts of zinc (40-100 ppm) to the diet, usually as zinc carbonate or sulphate.

Zinc deficiency symptoms have also been produced in chicks; these include retarded growth, poor feathering, poor calcification and skin lesions. Zinc is thought to be concerned in the processes of calcification and keratinisation.

Sources of Zinc

The element is fairly widely distributed. Yeast is a rich source, and zinc is concentrated in the bran and germ of cereal grains. The diets of ruminant animals are normally considered to contain adequate amounts of this element.

Zinc Toxicity

Although cases of zinc poisoning have been reported, most animals have a high tolerance for this element. Excessive amounts of zinc in the diet are known to depress food consumption and may induce copper deficiency.

MOLYBDENUM

Although molybdenum has been classed as an essential element in plant nutrition for some time, its main importance in animal nutrition was thought to be as a toxic rather than an essential element. The toxic role of molybdenum in the condition known as teart is described under the element Copper (p. 87). More recently molybdenum has been classed as an essential trace element, since it is known to be a constituent of the enzyme xanthine oxidase which plays an important part in purine metabolism. Molybdenum is also a component of nitrate reductase and of a bacterial hydrogenase.

Deficiency symptoms have not been reported under practical conditions. Recent experiments have demonstrated a growth-stimulating effect for molybdenum given to chicks and poult fed on purified

soya bean protein diets. A nutritional role of molybdenum has also been demonstrated in young lambs, where addition of the element as molybdate to a diet low in molybdenum increased liveweight gains. It has been suggested that this increase in liveweight might have been an indirect effect induced by stimulating cellulose breakdown in the rumen.

SELENIUM

Like molybdenum, selenium has always been regarded as an important element in animal nutrition because of its toxicity.

In certain areas of the U.S.A. selenium is responsible for the diseases known locally as 'alkali disease' and 'blind staggers'. Alkali disease is a chronic form of selenium poisoning, caused by the ingestion of certain species of plants which contain 10 to 30 ppm of selenium. The disease affects horses, cattle and sheep, and the symptoms include dullness, stiffness of the joints, lameness, loss of hair from mane or tail and hoof deformities. Blind staggers is an acute form of selenium poisoning which occurs in cattle and sheep after consumption of certain weeds such as *Astragalus bisulcatus*, which may contain up to 4000 ppm. Different plants vary in the amounts they take up from the soil, but usually the selenium content of the plant is related to the level of the element in the soil. A concentration of 5 ppm in foods or 0.5 ppm in milk or water may be potentially dangerous to farm animals.

Selenium toxicity has not been reported in Europe except in Eire. In Limerick high concentrations of the element are found in soils and plants, the soils involved being mildly acid or alkaline.

In seleniferous plants selenium replaces sulphur in the amino acids methionine and cystine and these selenium containing amino acids apparently replace methionine and cystine in body proteins. Hair, wool and hooves are normally rich in sulphur containing amino acids and are affected adversely by selenium toxicity.

It is known that the toxic effect of selenium is reduced when high protein foods are given to animals. Trace amounts of arsenic compounds also have a protective action.

In 1957 the role of selenium in animal nutrition assumed a new aspect when it was demonstrated that feeding with extremely small amounts (0.5 ppm) of selenium as sodium selenite prevented liver necrosis in rats. It was also shown that selenite prevented exudative diathesis in chickens. Liver necrosis produced by feeding pigs on a diet deficient in vitamin E could be cured by feeding with either vitamin E or sodium

selenite. Selenium compounds have been shown to prevent muscular dystrophy in lambs and calves (see Chapter 5). The exact function of selenium in the aetiology of these diseases is still unknown, but it is considered by many that there is sufficient evidence to regard selenium as an essential trace element. It should be remembered, however, that the margin between the toxic level and the dietary level required to prevent deficiency symptoms in animals is small, and for this reason it is inadvisable to add this element to mineral supplements for farm animals.

PROBABLY ESSENTIAL ELEMENTS

FLUORINE

Fluorine is distributed in traces throughout the body, but is concentrated in the bones and teeth. The importance of fluorine as a trace element in preventing dental caries has been well established, though evidence of its essential role in metabolism is still inconclusive. The element is very toxic, however, and an excess in the diet above 20 ppm of the dry matter causes a condition described as 'fluorosis' in which the teeth become pitted and worn until the pulp cavities are exposed; the teeth become sensitive to cold water, and the appetite declines, resulting in slow growth. Bone and joint abnormalities also occur. Fluorine is a cumulative poison, and the ingestion of small amounts over long periods of time may produce toxic symptoms. The commonest sources of danger from this element are fluoride-containing water and fluoride rock phosphates. Cases of fluorine toxicity have been reported in animals grazing in industrial areas where fluoride-containing smoke has contaminated pastures.

OTHER ELEMENTS

Recently it has been suggested that bromine, barium and strontium may have an essential function in animals, although conclusive evidence is still lacking. A possible essential role of bromine for chicks has been suggested; small but significant growth responses to trace additions of this element to semi-synthetic diets have been reported. Conclusive evidence that barium is a dietary essential for animals is not yet available; experiments with rats and guinea-pigs suggest that it may be essential for these species.

Considerable attention has been given recently to the element strontium because of the formation of radioactive [^{90}Sr] as a by-product

of nuclear fission. Limited evidence suggests that strontium may be a dietary essential for the growth of rats and guinea-pigs.

FURTHER READING

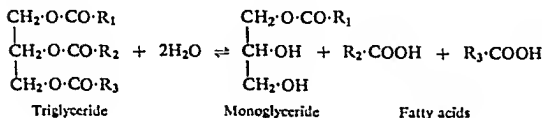
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Chapter 7

ENZYMES

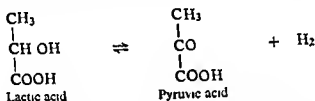
The existence of living things involves a continuous series of chemical changes. Thus green plants elaborate simple chemical compounds such as carbon dioxide and water into complex compounds like sugars, starch and proteins, and in doing so fix and store energy. Subsequently these compounds are broken down, by the plants themselves or by animals which consume the plants, and the stored energy is utilised. The complicated reactions involved in these processes are reversible, and when not associated with living organisms are often very slow; extremes of temperature and/or pressure would be required to increase their velocity to practicable levels. In living organisms such conditions do not exist. Yet the storage and release of energy in such organisms must take place quickly when required, and this necessitates a high velocity of the reactions involved. The required velocity is attained through the activity of numerous catalysts present in the organisms. A catalyst in the classical chemical sense is a substance which affects the velocity of a chemical reaction without appearing in the final products; characteristically the catalyst remains unchanged in mass upon completion of the reaction. The catalysts elaborated and used by living organisms are organic in nature and are known as enzymes. Each living cell contains hundreds of enzymes, and it is due to the coordinated action of these substances that the life processes are able to take place.

Catalytic action. Typical of enzyme-catalysed reactions are the hydrolyses of various substances such as fats and proteins which are essential for the normal functioning of the organism. A fat may be broken down to glycerides and fatty acids under the influence of a lipase:

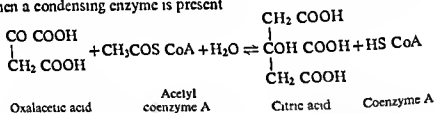


Such a reaction, which in the laboratory requires the action of strong alkalis at high temperatures, or superheated steam, takes place in the body at ordinary temperatures and without hydrolysing reagents. Similarly peptidases split proteins by hydrolysis of the peptide linkage between the constituent amino acids. Enzymes of this type are classed as *hydrolysing enzymes*.

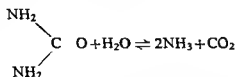
The other large group are the *transferring enzymes* which catalyse transfer reactions. These involve removal or addition of hydrogen, oxygen or electrons as in oxidation-reduction reactions, or of acetyl groups as in various acylation processes, as well as of phosphate groups in energy metabolism. Lactic acid is oxidised to pyruvic acid in muscle in the presence of lactic acid dehydrogenase.



Again, in the formation of citric acid from oxalacetic acid during the release of energy in the body, addition of an acetyl group takes place when a condensing enzyme is present.

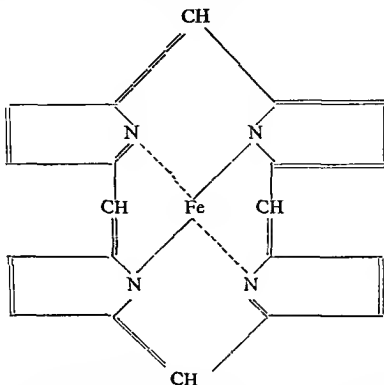


There are also a few miscellaneous enzymes catalysing reactions which do not fit into these large groups. Typical is the breakdown of urea by urease.

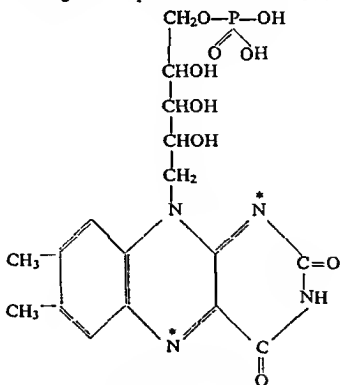


Nature of enzymes Many enzymes have now been isolated in the pure state and their structure elucidated. All have proved to be complex proteins of high molecular weight. Many of the proteins need special groups to aid their activity, especially in the case of the transfer enzymes. For example the cytochromes are important in certain oxidation reactions during which they accept electrons from a reduced

substance, which is consequently oxidised. The cytochromes are haem proteins, and as such contain the general grouping:



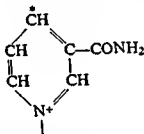
Without this iron-containing haem group the enzyme would be inactive, since electron exchange takes place at the iron atom. Such active



Flavin mononucleotide

groups are known as 'prosthetic' groups when they are actually part of the enzyme molecule; the remainder of the molecule is then known as the apo-enzyme, and the whole molecule as the holo-enzyme. The prosthetic group need not necessarily contain an inorganic entity but may be entirely organic, as in the case of the flavoproteins, which contain flavin mononucleotide (FMN) as the active group. Exchange of hydrogen atoms during oxidation and reduction takes place at the positions marked *.

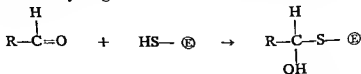
Sometimes the enzyme needs for its activity a group which is a separate entity. In the oxidation of lactic acid to pyruvic acid the hydrogen released must be removed. This is done by a substance nicotinamide-adenine dinucleotide (NAD) or nicotinamide-adenine dinucleotide phosphate (NADP), which contain the nicotinamide grouping:



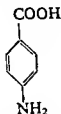
The hydrogen exchange takes place at the position marked *.

Such substances as NAD and NADP are known as 'coenzymes', and several enzymes may have the same coenzyme. The acetylation of oxalacetic acid depends upon donation of an acetyl group by acetyl coenzyme A, which reverts to coenzyme A, this can be reacylated and again take part in an acetylation. In the absence of the coenzyme the condensing enzyme would be quite inactive. Many enzymes require the presence of metal ions in order to 'activate' the enzyme. Such metal ions are known as *actuators*. Arginase, for example, needs manganese ions for its action.

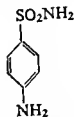
Mechanism of enzyme action. Enzyme action involves the formation of a complex between the enzyme and the substrate, the substance to be acted upon. Such complexes will be formed between the substrate and a relatively few active centres on the enzyme. The bond may take a variety of forms, from the chemical bond, typified by sulphydryl groups on the enzyme (E)



of sulphanilamide This competes with the similar para-amino benzoic acid in certain reactions essential for bacterial growth.



Para amino benzoic acid



Sulphanilamide

Inhibition of enzyme action may also result from the presence of arsenic and of heavy metals such as mercury and silver, which block the active groups of the enzyme

Temperature As in other chemical reactions, the efficiency of enzyme-catalysed reactions is increased by raising the temperature. Very approximately, the speed of reaction is doubled for each increase of 10°C . As the temperature rises, however, a complicating factor comes into play, in that denaturation of the enzyme protein begins. This is a molecular rearrangement which causes a loss of the active centres of the enzyme surface and results in a loss of efficiency. Above 50°C the destruction of the enzyme becomes more rapid, and all enzymes are destroyed when heated to 100°C . The time for which the enzyme is subjected to a given temperature affects the extent of efficiency loss. As would be expected, all enzymes have a temperature range within which they are most efficient.

Acidity Hydrogen ion concentration also has an important effect on the efficiency of enzyme action. Many enzymes are most effective in the region of pH 6 to 7, which is that pertaining to the cell. Extra cellular enzymes show maximum activity in the acid or the alkaline pH range, but in any case the actual range of pH within which the enzyme works is only about 2.5 to 3.0 units, outside this range the activity drops off very rapidly. The reduction in efficiency caused by changes in the pH is due to changes in the degree of ionisation of the substrate and enzyme. Where the linkage between the active centres is electrostatic, this affects the facility with which the intermediate complex is formed and thus the efficiency of enzyme action.

Nomenclature of Enzymes

Some enzymes were named in the early days of enzyme study and have unsystematic names such as those of the digestive enzymes

'pepsin', 'trypsin' and 'ptyalin'. Nowadays it is usual, when naming enzymes, to indicate the type of reaction catalysed and the nature of the substrate. The suffix -ase is added to the name to denote an enzyme. Typical of the modern system is the name 'lactic acid dehydrogenase'.

FURTHER READING

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Chapter 8

DIGESTION

Many of the organic components of food are in the form of large insoluble molecules which have to be broken down into simpler compounds before they can pass through the mucous membrane of the alimentary canal into the blood and lymph. The breaking down process is termed 'digestion', the passage of the digested nutrients through the mucous membrane 'absorption'.

The processes important in digestion may be grouped into mechanical, chemical and microbial. The mechanical activities are mastication and the muscular contractions of the alimentary canal. The main chemical action is brought about by enzymes secreted by the animal in the various digestive juices, though it is possible that plant enzymes present in unprocessed foods may in some instances play a minor role in food digestion.

Microbial digestion of food, also enzymic, is brought about by the action of bacteria and protozoa, micro organisms which are of special significance in ruminant digestion. In simple stomached animals microbial activity occurs in the large intestine.

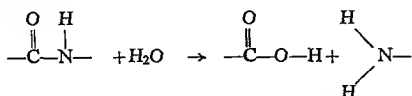
DIGESTIVE ENZYMES

The enzymes secreted into the digestive tract break down food by hydrolysis, and with the exception of the proteolytic enzymes, pepsin and rennin have an optimum pH within the range 6-8.

Many of the digestive enzymes are initially present in the secretions in the form of inactive precursors (zymogens) which are activated after secretion into the tract.

Carbohydrases These enzymes hydrolyse the glycosidic linkages between sugar units, and are usually highly specific. The α amylases hydrolyse the α 1,4-glucosidic linkages of glycogen and starch. Maltase, sucrase, lactase and trehalase are specific enzymes which hydrolyse maltose, sucrose, lactose and trehalose respectively. Oligo-1,6 glucosidase hydrolyses α 1,6 linkages in dextrans produced after amylase activity.

Proteolytic enzymes. These enzymes are concerned with hydrolysis of the peptide link



Proteolytic enzymes are usually divided into two main groups, the *endopeptidases*, which generally act upon peptide linkages that are

TABLE 8 1 Main Digestive Enzymes

Name	Source	Substrate
<i>Enzymes hydrolysing peptide links</i>		
Pepsin	Gastric mucosa	Proteins and certain peptides
Rennin	Gastric mucosa (young calves)	Proteins and certain peptides
Trypsin	Pancreas	Proteins and certain peptides
Chymotrypsin	Pancreas	Proteins and certain peptides
Carboxypeptidase	Pancreas	Certain peptides
Elastase	Pancreas	Elastin and other proteins
Aminopeptidases	Small intestine	Certain peptides
Dipeptidases	Small intestine	Dipeptides
<i>Enzymes hydrolysing ester links</i>		
Gastric lipase	Gastric mucosa	Fats and other organic esters
Pancreatic lipase	Pancreas	Fats and other organic esters
<i>Enzymes hydrolysing glycoside links</i>		
α Amylase	Saliva, pancreas	Starch, glycogen, dextrins
Sucrase	Small intestine	Sucrose
Maltase	Small intestine	Maltose
Lactase	Small intestine	Lactose
Trehalase	Small intestine	Trehalose
Oligo-1,6-glucosidase	Small intestine	Dextrins

situated away from the end of the substrate molecule, and *exopeptidases*, which act on peptide linkages at the end of a peptide chain and which are near to a free carboxyl or amino group. Endopeptidases were originally termed proteases, and include pepsin, rennin, trypsin and chymotrypsin.

Pepsin preferentially attacks peptide linkages involving the amino group of an aromatic amino acid (phenylalanine or tyrosine) in proteins or peptides, pepsin is less specific, however, than other endopeptidases and can hydrolyse other linkages. Rennin is a milk-coagulating enzyme, similar to pepsin in activity, which occurs in the gastric secretion of the calf and probably other young ruminants. Trypsin has a preferential specificity towards peptide bonds involving the carboxyl group of arginine and lysine, while chymotrypsin is most active towards the peptide linkage involving the carboxyl group of the aromatic amino acids. Exopeptidases include carboxypeptidase, which acts on polypeptides, splitting off the terminal amino acid which has a free α carboxyl group, aminopeptidases, which act on the peptide bond adjacent to the free amino group of simple peptides, and dipeptidases, which specifically act only on certain dipeptides.

Esterases The breakdown of fats is brought about by the enzyme lipase. In contrast to the other digestive enzymes lipase is not very specific, and can attack a wide range of glycerides. The main digestive enzymes are shown in Table 8.1

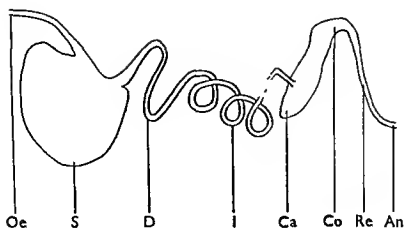
DIGESTION IN THE PIG

The alimentary canal The various parts of the alimentary canal of the pig are shown in Fig. 8.1. The secretions entering the tract are produced in the salivary, gastric, pancreatic and intestinal glands and the liver. The movement of the intestinal contents along the tract is produced by peristaltic waves, which are contractions of the circular muscle of the intestine. A number of different kinds of movements of the intestinal wall are recognised, the functions of these being to move the contents along the tract, to mix the digestive juices with the food, and to bring the digested nutrients into contact with the intestinal mucous membrane for subsequent absorption.

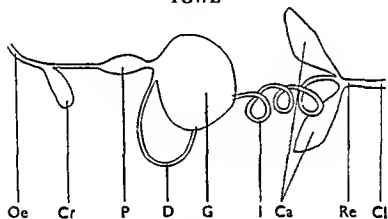
The small intestine is the main absorption site, and contains a series of finger-like projections, the villi, which increase the absorption area. Each villus contains an arteriole and venule, together with a drainage tube of the lymphatic system, a lacteal. The venules ultimately drain into the portal system and the lacteals into the thoracic duct.

Digestion in the mouth The digestion occurring in the mouth is mainly mechanical in nature. Mastication is important in two ways: it helps to break up large particles of food, and it also mixes food with saliva, which acts as a lubricant. Saliva is secreted by three pairs of salivary glands: the parotids, which are situated in front of each

FIG



FOWL



COW

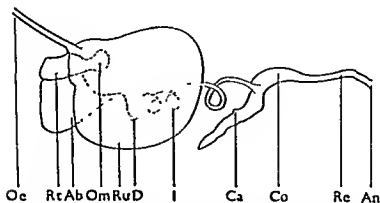


FIG. 8.1. Diagrammatic representation of the digestive tracts of different farm animals.

An = Anus. Ab = Abomasum. Ca = Caecum. Cl = Cloaca. Co = Colon. Cr = Crop. D = Duodenum. G = Gizzard. I = Ileum. Oe = Oesophagus. Om = Omasum. P = Proventriculus. Re = Rectum. Rt = Reticulum. Ru = Rumen. S = Stomach.

car, the submaxillary glands which lie on each side of the lower jaw, and the sublingual glands, which are underneath the tongue

Saliva is about 99 per cent water, the remaining 1 per cent consisting of mucin, inorganic salts and the enzyme, α amylase (ptyalin) The pH of pig's saliva is about 7.3, which is only slightly above the value regarded as optimal for the activity of α -amylase It is doubtful however if much enzymic digestion occurs in the mouth, since the food is quickly swallowed and passes along the oesophagus to the stomach Some starch digestion by salivary amylase can take place in the stomach, since the food mass is not at once mixed with the gastric juice

Digestion in the stomach The stomach of the adult pig has a capacity of about 8 litres, and consists of a single compartment which functions not only as an organ for the digestion of food but also for storage The gastric glands are present in the mucous membrane of the stomach and secrete gastric juice, which consists mainly of water, inorganic salts, mucus, hydrochloric acid and pepsinogen, the precursor of the enzyme pepsin The acid concentration in the gastric secretion varies on different diets but is generally about 0.1 N, and is sufficient to lower the pH value of the stomach contents to about pH 2.0 The acid acts as an activator of pepsinogen, converting it into the proteolytic enzyme, pepsin

Traces of the enzyme lipase may be present in the gastric secretion, but it is unlikely that this enzyme can hydrolyse fats in the stomach since it is not active in the presence of strong acid

A number of factors are concerned in the stimulation of the gastric glands to secrete gastric juice, among them being the presence of food in the stomach

Digestion in the small intestine Four secretions enter the small intestine pancreatic juice duodenal juice, succus entericus and bile

The pancreatic juice is secreted by the pancreas, a gland which lies in the duodenal loop and opens into the duodenum by means of the pancreatic duct The pancreatic juice contains inorganic salts (mainly sodium bicarbonate) α amylase lipase, trypsinogen, chymotrypsinogen and procarboxypeptidase The pancreas is stimulated to secrete its juice by a number of factors hydrochloric acid, starch, fats and the hormone *secretin* Secretin is produced by the action of the acid from the stomach on *prosecretin*, which occurs in the epithelial cells of the small intestine Trypsinogen is converted into trypsin by an enzyme enterokinase present in the succus entericus This activation of the precursor is also catalysed by trypsin itself A reaction of this type in which the product acts as a catalyst is described as *autocatalytic*

Chymotrypsinogen and procarboxypeptidase are activated into chymotrypsin and carboxypeptidase respectively by the presence of trypsin.

The pancreatic juice also contains lipase, which breaks down fats to mono- and di-glycerides and fatty acids. Complete hydrolysis with the production of glycerol probably occurs to only a limited extent (see p. 112). The only carbohydrase present in the pancreatic juice in significant amounts is α -amylase, which hydrolyses glycogen and starch to glucose, maltose and short-chain dextrins (limit dextrins).

The duodenal (Brunner's) glands produce a secretion which enters the duodenum by means of ducts situated between the villi. This secretion does not contain enzymes, but acts as a lubricant and also protects the walls of the duodenum from hydrochloric acid entering from the stomach.

The other secretion from the small intestine is the succus entericus, produced in the crypts of Lieberkuhn, which are tubular depressions between the villi. Succus entericus contains lipase, enterokinase, aminopeptidases, dipeptidases and the carbohydrases—maltase, sucrase, lactase, trehalase and oligo-1,6-glucosidase. The crypts of Lieberkuhn are stimulated to secrete succus entericus by mechanical stimulation of the mucosa and also by the presence of the hormone, *enterocrinin*, which is secreted by the liver and passes along the bile duct into the duodenum.

Bile, which is secreted by the liver and passes along the bile duct into the duodenum, does not contain enzymes, but contains the sodium and potassium salts of bile acids, chiefly glycocholic acid and taurocholic acid, and the bile pigments biliverdin and bilirubin. The bile salts play an important part in digestion by activating pancreatic and intestinal lipases and assisting in the emulsification of fats. In order for lipase to act efficiently it is necessary for fat to be emulsified or broken down into small particles, thereby producing a much larger surface upon which the enzyme can act. Bile also assists in the absorption of fatty acids and fat-soluble vitamins.

Pigs, cattle and sheep all possess a gall bladder in which the bile is stored until required.

Digestion in the large intestine. The main site of absorption of digested nutrients is the small intestine, so that by the time the food material has reached the entrance to the colon most of the hydrolysed nutrients will have been absorbed. With normal diets there is always a certain amount of material which is resistant to the action of the enzymes secreted into the alimentary canal. Cellulose and many of the hemicelluloses are not attacked by any of the enzymes present in the digestive

secretions of the pig. Lignin is known to be completely unaffected and is thus indigestible. It is also conceivable that lignified tissues may trap proteins and carbohydrates and protect them from the action of digestive enzymes. The glands of the large intestine are mainly mucous glands which do not produce enzymes, and digestion in the large intestine is therefore brought about by enzymes which have been carried down in the food from the upper part of the tract, or occurs as a result of microbial activity.

Conditions in the small intestine are unfavourable for rapid development of bacteria, but in the large intestine, particularly in the caecum, there is extensive microbial activity. The bacteria in the large intestine are mainly of the proteolytic type which attack undigested proteins and produce a number of products including skatole, indole, phenol, fatty acids, hydrogen sulphide and amino acids. In the pig it is known from digestibility studies that the cellulose of certain foods is broken down to a limited extent, this microbial breakdown is generally thought to occur in the large intestine. The digestion of cellulose and other higher polysaccharides is nevertheless small compared with that taking place in the horse and ruminants, which have a digestive system adapted to deal with fibrous foods. The products of this microbial breakdown of polysaccharides are not sugars but mainly the volatile fatty acids, acetic, propionic and butyric.

Bacterial action in the large intestine may have a beneficial effect due to the synthesis of some of the B vitamins, which may be absorbed and utilised by the host. Synthesis of most of the vitamins in the digestive tract of the pig is, however, insufficient to meet the daily requirements and a dietary source is needed.

The waste material, or faeces, voided from the large intestine via the anus consists of water, undigested food residues, digestive secretions, epithelial cells from the tract, bacteria, inorganic salts, indole, skatole and other products of bacterial decomposition.

Digestion in the Young Pig

From birth until about the age of five weeks the concentration and activity of many of the digestive secretions in the young pig are different from those in the tract of the adult animal.

Pepsin activity is low at birth and increases markedly after three weeks of age. α -Amylase activity in the small intestine increases during the first ten days. Maltase and sucrase activities are low at birth, while lactase is high and decreases as the animal matures. Table 2 shows the activity of some of the important carbohydrases in the young pig.

These differences in enzyme activities are of special significance where piglets are reared on early weaning diets. If young pigs are weaned at 14 days of age, their diet, especially regarding the types of carbohydrates, should be different from that for older animals weaned at 5-6 weeks. Early weaning mixtures usually include a high proportion of dried milk products containing lactose.

TABLE 8.2. Weight of Disaccharide Hydrolysed per kg. Bodyweight per Hour by Small Intestine Enzymes in Young Pigs

	<i>Lactose (g)</i>	<i>Sucrose (g)</i>	<i>Maltose (g)</i>
Newborn	5.9	0.06	0.3
Five weeks	0.8	1.3	2.5

DIGESTION IN THE FOWL

The digestive tract of the fowl differs in a number of respects from that of the pig (see Fig. 8.1). In the fowl the lips and cheeks are replaced by the beak, the teeth being absent. The crop or diverticulum of the oesophagus is a pear-shaped sac whose main function is to act as a reservoir for holding food, although some microbial activity occurs there and results in the formation of organic acids. The oesophagus terminates at the proventriculus or glandular stomach, which leads into the gizzard, a muscular organ which undergoes rhythmic contractions and grinds the food with moisture into a smooth paste. The gizzard, which has no counterpart in the pig, although it is often compared to the pyloric part of the mammalian stomach, leads into the duodenum, which encloses the pancreas as in mammals. The pancreatic and bile ducts open into the intestine at the termination of the duodenum. Where the small intestine joins the large intestine there are two large blind sacs known as the caeca. The large intestine is relatively short and terminates in the cloaca, from which urine and faeces are excreted together.

The enzymes present in the digestive secretions of the fowl are similar to those in the secretions of mammals, although lactase has not been detected. Salivary α -amylase is known to occur in the fowl, and the action of this enzyme on starch continues in the crop.

The presence of grit in the gizzard, although not essential, has been shown to increase the breakdown of whole grains by about 10 per cent.

The pancreatic juice of fowls contains the same enzymes as the

mammalian secretion, and the digestion of proteins, fats and carbohydrates in the small intestine is believed to be similar to that occurring in the pig. The intestinal secretion contains mucin, α -amylase, maltase, sucrase and proteolytic enzymes.

The caeca, which function mainly as absorptive organs, are not essential to the fowl, since surgical removal causes no harmful effects. Recent experiments with adult fowls indicate that the cellulose present in cereal grains is not broken down by microbial activity to any extent during its passage through the digestive tract, although some hemi-cellulose breakdown occurs.

ABSORPTION OF DIGESTED NUTRIENTS

Carbohydrates The digestion of carbohydrates by enzymes secreted by the pig results in the production of monosaccharides. These simple sugars are normally absorbed through the walls of the small intestine into the portal blood system and are then transported to the liver. Absorption of volatile fatty acids resulting from microbial digestion occurs in the large intestine.

In the fowl, it is known that sugars and fermentation products can be absorbed from the crop.

The exact process of the absorption of hexoses from the intestine is still uncertain, but it is thought that hexose phosphates are formed in the cells of the intestinal mucosa and then broken down again before entering the blood. The rates of absorption for different sugars are known to vary considerably, the pentose sugars having a much slower rate of absorption than the hexoses.

Fats Two separate theories have been put forward to explain the manner in which fat is absorbed from the small intestine. According to the *lipolytic hypothesis*, which is the original view, fats after emulsification are hydrolysed by the enzyme, lipase, into fatty acids and glycerol. These components then pass into the epithelial cells of the intestinal mucosa, where the fatty acids are combined with glycerol to produce neutral fat again. These fine globules of fat pass into the lacteals of the villi, enter the thoracic duct and join the general circulation. It is generally considered that phosphorylation is of considerable importance in this process of absorption.

According to the more recent *partition theory* of fat absorption, only part of the ingested fat is hydrolysed in the intestine, mono- and di-glycerides being produced. The triple combination of fatty acid, bile salt, monoglyceride is an ideal emulsifying agent under the

conditions existing in the upper part of the small intestine, and the fat is reduced to a fine emulsion of particle size less than 0.5 microns in diameter. In this fine state the particles of fat can be absorbed through the intestinal wall into the lymphatic system. One of the arguments put forward in favour of the partition theory is that the enzyme, lipase, would be able to hydrolyse only a small amount of the dietary fat in the short time that it remained in the small intestine.

Proteins. The main products of protein digestion are amino acids, and the main site of absorption is the small intestine. Thence the amino acids pass into the portal blood and thence to the liver.

Minerals. The absorption of mineral elements from the digestive tract is governed by many factors, but principally by the solubility of the element in contact with the absorbing membrane.

In the case of calcium and phosphorus, an excess of either interferes with the absorption of the other. Vitamin D is known to promote the absorption of both calcium and phosphorus. It is known also that certain organic compounds such as the phosphorus-containing phytic acid form insoluble calcium and magnesium salts (phytates) which are broken down with difficulty; this is of special significance in poultry nutrition, where phytates are poorly utilised by the chick (see p. 79).

The presence of oxalic acid in plants tends to render the calcium unavailable by forming insoluble calcium oxalate. It is difficult however to generalise about the effects of these insoluble organic compounds, since there are species differences in the degree of breakdown of these materials, and there is also evidence that phytates and oxalates are broken down in the rumen.

The absorption of magnesium has received considerable attention recently in connection with the aetiology of hypomagnesaemic tetany. Studies with [^{25}Mg] indicate that absorption of this element from the tract of ruminants is frequently low, and as much as 90 per cent. of the ingested magnesium in herbage may be unavailable to the ruminant.

The absorption of iron is to a large extent independent of the dietary source. The animal has difficulty in excreting iron from the body in any quantity, and therefore a method exists of regulating the iron absorption to prevent excessive amounts entering the body (see p. 86). In adults the absorption of the element is generally low, but after severe bleeding and during pregnancy the requirement for iron is increased, so that absorption of the element is also increased. Anaemia due to iron deficiency may, however, develop on iron-low diets. Experiments carried out with dogs have shown that the absorption of iron by

anaemic animals may be 20 times as great as that by normal healthy dogs. It is generally believed that iron must be in the ferrous form before absorption can occur, and certain naturally occurring reducing agents such as vitamin C favour iron absorption by reducing the ferric ion to the ferrous.

Zinc resembles iron in being poorly absorbed from the alimentary canal. Calcium is believed to inhibit the absorption of zinc.

Iodine is present mainly as inorganic iodide in plants, whereas in foods of animal origin it exists partly in an organic form. It is thought that the iodine in organic combination is less well absorbed than the inorganic form.

Vitamins Vitamin A is more readily absorbed from the digestive tract than its precursor carotene, although it is thought that vitamin A esters must first be hydrolysed by an esterase to the alcohol form before being absorbed. The main site of carotene absorption is the small intestine, and the bile salts play an important part in this process. The absorption of vitamins D, E and K is also governed by the presence of bile. Phytosterols are poorly absorbed, and it is generally considered that unless ergosterol has been irradiated to vitamin D₂ before ingestion it cannot be absorbed from the tract in any quantity.

DIGESTION IN THE RUMINANT

The stomach of the ruminant is divided into four compartments (see Fig 8.1). In the young suckling the first two compartments, the rumen and its continuation the reticulum, are relatively undeveloped, and milk reaching the stomach is channelled by a tube like fold of tissue, known as the oesophageal groove, directly to the third and fourth compartments, the omasum and abomasum. As the calf or lamb begins to eat solid food the first two compartments (often considered together as the reticulo rumen) enlarge greatly, until in the adult they comprise 85 per cent of the total capacity of the stomach. In the adult the oesophageal groove no longer functions and food passes into the reticulo rumen.

The food is diluted by copious amounts of saliva and the contents of the rumen often exist in two phases, a lower liquid phase in which the finer food particles are suspended and an upper one of coarser, solid material. The breakdown of food is accomplished partly by physical and partly by chemical means. The contents of the rumen are continually mixed by the rhythmic contractions of its walls, and the coarser material arriving at the anterior end when the animal is ruminating will

be regurgitated, chewed and returned to the rumen. Chemical breakdown is brought about by enzymes, but the enzymes acting in the reticulo-rumen are secreted not by the animal itself but by bacteria and protozoa.

The bacteria number 10^9 to 10^{10} per ml of rumen contents. Many

TABLE 8.3. Some common Species of Rumen Bacteria, Classified according to the Reactions they Bring about *in vitro*

Type of organism	Name	Description	Substances produced
Cellulose-fermenting	<i>Bacteroides succinogenes</i>	Gram negative rods	Mainly acetic and succinic acids
	<i>Rununococcus flavefaciens</i>	Gram negative, catalase negative streptococci, with yellow colonies	Acetic, succinic and lactic acids
Starch- and sugar-fermenting	<i>Streptococcus bovis</i>	Gram positive, capsulated	Lactic acid and polysaccharides
	<i>Butyrivibrio fibrisolvens</i>	Gram negative, slightly curved rods	Butyric, formic and lactic acids
	<i>Succinivibrio dextrinosolvens</i>	Gram negative, curved rods	Succinic, formic and acetic acids
	<i>Bocteroides rumenicola</i>	Gram negative, oval or rod	Succinic, formic and acetic acids
	<i>Selenomonas rumunantium</i>	Gram negative, bean-shaped	Lactic, propionic and acetic acids
Lactic acid- and succinic acid-fermenting	<i>Veillonella gazogenes</i>	Gram positive micrococcus	Propionic and acetic acids
	<i>Peptostreptococcus elsdenii</i>	Gram negative, non-motile	Fatty acids from C ₂ to C ₆
Vitamin-synthesising	<i>Flavobacterium eitarumen</i>		B group vitamins
	<i>Clostridium butyricum</i>	Gram positive, spore-forming rods	B group vitamins

different species and strains have been recognised and isolated, and for descriptions of them the reader is referred to the works listed at the end of this chapter. Some of the better known species are given in Table 8.3, where they are grouped according to the food constituents they attack and to the substances they produce. The total number of bacteria in the rumen and the types which predominate at any one time depend on the nature of the host's diet. The highest total counts have been recorded with diets largely composed of concentrates; diets rich in soluble carbohydrates encourage the growth of lactobacilli.

A normal rumen flora is established quite early in life—as early as six weeks of age in calves

Protozoa are present in smaller numbers (10^6 per ml), but as they are larger than bacteria they may equal the latter in total bulk. Two broad categories are recognised. The oligotrichs can ingest food particles and can utilise both simple and complex carbohydrates, including cellulose. The holotrichs on the other hand do not generally ingest food particles and cannot utilise cellulose. The breakdown of foods apparently accomplished by protozoa is to some extent attributable to the bacteria they take in with food particles (protozoa have thus been described as 'micro ruminants')

The great activity of rumen micro organisms is illustrated by the fact that of the digestible dry matter entering the rumen only about 30 per cent continues its passage through the alimentary canal. The remaining 70 per cent is converted by the micro organisms into soluble and gaseous compounds which are absorbed directly from the rumen into the blood or, in the case of gases, lost by eructation (belching).

The combined contractions of the rumen and reticulum are instrumental in washing finer particles of food through to the omasum. Here water is absorbed from the digesta before they enter the abomasum. In this last compartment, which corresponds to the simple stomach of the pig, gastric juice containing pepsin is secreted. From the abomasum onwards the processes of digestion and absorption are similar in the ruminant to those in simple stomached animals.

Digestion of carbohydrates in the rumen The diet of the ruminant contains considerable quantities of cellulose, hemicelluloses and other carbohydrates which are not attacked by the digestive enzymes secreted by animals. Thus in young pasture herbage, which is frequently the sole food, about 40 per cent of the dry matter consists of cellulose and hemicelluloses, while in more mature herbage, hay and straw, the proportion is generally higher. The cellulose is associated with a varying amount of lignin. It has been recognised since about 1880 that cellulose and hemicelluloses, but not lignin, are attacked by rumen micro-organisms and digested to the extent of at least 50 per cent and possibly 80 per cent. The important products of the process were for a long time thought to be monosaccharides, but it is now known that if these are formed they are almost completely fermented to a mixture of organic acids and the gases, carbon dioxide and methane. Furthermore it is now well established that starch and soluble sugars entering the rumen are readily broken down in the same manner.

The main end products of carbohydrate breakdown in the rumen are

acetic, propionic and butyric acids. Higher acids such as valeric are also formed, but in much smaller amounts. The processes giving rise to these acids are complex and not fully understood. From Table 8.3 it would appear that succinic and lactic acids are important intermediates, and these can in fact be detected in the rumen liquor. The total concentration of volatile fatty acids in rumen liquor varies between 0.2 and 1.5 g per 100 ml according to the animal's diet and the time that has elapsed since the previous meal. The relative proportions of the acids also vary, and some typical figures are shown in Table 8.4.

TABLE 8.4 Volatile Fatty Acids (VFA) in the Rumen of Cattle and Sheep Fed on various Diets

<i>Animal</i>	<i>Diet</i>	<i>Total VFA (m moles/ litre)</i>	<i>Individual VFA (molecular proportions)</i>			<i>Higher acids</i>
			<i>Acetic</i>	<i>Propionic</i>	<i>Butyric</i>	
Cow	Silage (70 lb)	108	74	17	7	3
"	Pasture herbage	143	66	18	12	4
"	Hay (16 lb) + concentrates (20 lb)	136	58	24	13	6
"	Hay (2 lb) + concentrates (24 lb)	139	41	38	9	12
"	Steamed maize	129	34	46	6	14
Sheep	Lucerne hay	—	67	23	7	4
"	Dried grass	—	58	22	9	2
"	Maize	89	46	32	18	4

The predominant acid is acetic, and roughage diets, high in cellulose, give rise to acid mixtures particularly high in acetic acid. As the proportion of concentrates in the diet is increased, the proportion of acetic acid falls and that of propionic rises. The total weight of acids produced may be as high as 3 kg per day in cows. Much of the acid produced is absorbed directly from the rumen, reticulum and omasum, although some may be expected to pass through the abomasum and be absorbed in the small intestine. In addition some of the products of carbohydrate digestion in the rumen are used by bacteria and protozoa to form their own cellular polysaccharides, but the amounts passing to the small intestine are probably small and hardly significant.

The rate of gas production in the rumen is most rapid immediately after a meal and in the cow may exceed 30 litres per hour. Carbon dioxide is produced partly as a by-product of fermentation and partly by the reaction of organic acids with the bicarbonate present in the

saliva Methane most probably arises from the reduction of carbon dioxide, about 4.5 g being formed for every 100 g of carbohydrate digested

Most of the gas produced is lost by eructation, if gas accumulates it causes the condition known as bloat, in which the distension of the rumen may be so great as to result in the collapse and death of the animal. Bloat occurs most commonly in dairy cows grazing on young, clover-rich herbage, and is due not so much to excessive gas production as to the failure of the animal to eructate. Frequently the gas is trapped in the rumen in a foam, whose formation may be promoted by substances present in the clover. It is also possible that the reflex controlling eructation is inhibited by a physiologically active substance which is present in the food or formed during fermentation. Bloat is a particularly serious problem in New Zealand, where it is prevented by dosing the cows or spraying the pasture with anti-foaming agents such as vegetable oils, or by suppressing rumen fermentation by the oral administration of large doses of penicillin.

The extent to which cellulose is digested in the rumen depends particularly on the degree of lignification of the plant material. Lignin is itself resistant to bacterial attack and appears to hinder the breakdown of the cellulose with which it is associated. Thus, in young pasture grass containing only 5 per cent lignin in the dry matter, 80 per cent of the cellulose may be digested, but in older herbage with 10 per cent lignin the proportion of cellulose digested may be less than 60 per cent. Cellulose digestion is also reduced by increasing the amounts of starch or sugars in the diet.

The breakdown of cellulose and other resistant polysaccharides is undoubtedly the most important digestive process taking place in the rumen. Besides contributing to the energy supply of the ruminant, it ensures that other nutrients which might escape digestion are released from the plant cells and exposed to enzyme action. Although the main factor in the process is the presence of micro-organisms in the rumen, there are other factors of importance. The great size of the rumen allows food to accumulate and ensures that sufficient time is allowed for the rather slow breakdown of cellulose. In addition, the movements of the reticulo-rumen and the act of rumination play a part by breaking up the food and exposing it to attack by micro-organisms.

Digestion of protein Food proteins are hydrolysed to peptides and amino acids by rumen micro-organisms, but some of the amino acids are further degraded, by deamination, to organic acids, ammonia and carbon dioxide (see Fig. 8.2). The ammonia produced may be absorbed

from the rumen into the blood, carried to the liver and converted into urea (see Chapter 9). Some urea is returned to the rumen via the saliva but the greater part is excreted in the urine, and so the deamination of amino acids in the rumen represents a potentially serious tax on the protein of the ruminant's diet. Fortunately, however, the degradative activities of the rumen organisms are to a large extent balanced by their synthetic activities, in which they build up microbial protein from both amino acids and from simpler sources of nitrogen—from the ammonia arising from deamination and from the non-protein nitrogen of the food. When the organisms are carried through to the abomasum and small intestine their cell proteins are digested and absorbed. An important feature of the formation of microbial protein is that bacteria are capable of synthesising essential as well as non-essential amino acids, thus rendering their host independent of dietary supplies of the former.

The proportion of the food protein attacked in the rumen is unknown,

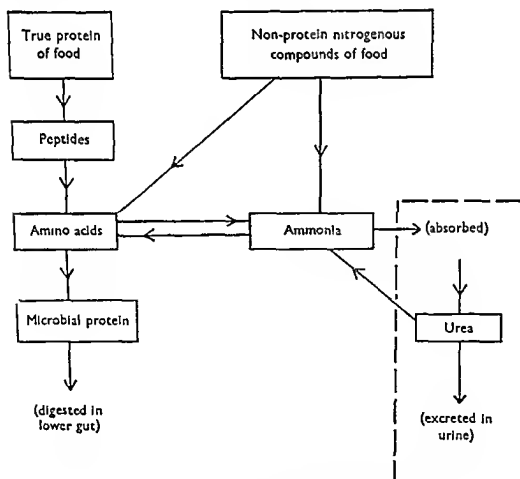


FIG. 8.2. Digestion and metabolism of nitrogenous compounds in the rumen.

but it is likely to be higher than 50 per cent and perhaps as high as 90 per cent. Consequently both the quantity and quality of the amino acid mixture eventually absorbed by the ruminant will depend very much on the balance of the rumen activities. On the one hand, deamination may result in a net loss of nitrogen and, therefore, of protein, on the other, the synthesis of protein from the non protein nitrogen of the food may produce a net gain. In either case the amino acid composition of the protein reaching the intestine is likely to be quite different from that of the original food protein.

The significance of deamination and the absorption of ammonia from the rumen has only recently been recognised. The quantity of nitrogen wasted in this way will depend particularly on the rate of production of ammonia in the rumen and the rate at which it is 'trapped' by synthesis of bacterial protein. Ammonia production is greater with high protein diets, particularly when the protein is soluble and therefore readily attacked. Ammonia utilisation is stimulated by a high level of soluble carbohydrates, particularly starch, in the diet, since these supply the bacteria with the energy needed for protein synthesis. On diets high in soluble protein and low in soluble carbohydrate the amount of nitrogen leaving the rumen as ammonia may be very great. A value of 14 g nitrogen per day has been suggested for a sheep fed on hay with a supplement of casein, this is equivalent to 88 g crude protein—considerably more than the maintenance requirement of the animal.

Utilisation of non protein nitrogen by the ruminant In theory, the ruminant could exist without dietary protein if it were provided with nitrogen in an inorganic or simple organic form from which the rumen organisms could synthesise protein. In practice, ruminants receive most of their food nitrogen as protein, but in recent years it has become an acceptable procedure to replace a part of the dietary protein with simpler nitrogen-containing substances, particularly urea. The substitution is made for economic reasons and is popular in areas where protein rich foods are scarce and expensive, such as the desert ranges of Australia.

Urea entering the rumen is rapidly broken down to ammonia, and so the extent to which it is used for protein synthesis will depend on those factors discussed above which influence the 'trapping' of ammonia by rumen organisms. Thus urea is most efficiently utilised when the diet is relatively low in nitrogen and high in starch. In general, not more than one quarter of the animal's requirements for protein should be met by urea nitrogen, with greater amounts the conversion

to protein is often very inefficient, because of the absorption of ammonia from the rumen. Furthermore the consumption of excessive quantities of urea, or even of normal amounts in a short space of time, can be toxic to the animal.

Digestion of lipids. The fats present in the food of ruminants are characteristically 'soft' and contain a high proportion of residues of the C_{18} poly-unsaturated acids, linoleic and linolenic. Although there is evidence of considerable hydrolysis of lipids in the rumen, the more interesting modification of dietary lipids effected by rumen organisms is the hydrogenation or 'barding' of unsaturated fatty acids. This process is of considerable importance in determining the composition of animal body fats, which are rich in the saturated C_{18} acid, stearic. Thus the body fat of the grazing bullock is generally harder than that of the horse on the same diet.

Synthesis of vitamins. The synthesis by rumen micro-organisms of all members of the vitamin B complex and of vitamin K has already been mentioned (see Chapter 5). In ruminants receiving foods well supplied with B vitamins the amounts synthesised are relatively small, but they increase if the vitamin intake in the diet decreases. The adult ruminant is therefore independent of a dietary source of these vitamins, but it should be remembered that adequate synthesis of vitamin B_{12} will take place only if there is sufficient cobalt in the diet.

MICROBIAL DIGESTION IN THE HORSE

Although the great size of its modified alimentary tract and its large population of micro-organisms make the ruminant pre-eminent as a digester of bulky foods, there are other domestic animals possessing these facilities to a lesser degree in which a considerable proportion of the food may undergo microbial digestion. Even the pig, with its short and simple tract, harbours sufficient micro-organisms in its large intestine to digest more than half of the cellulose in concentrated foods.

The horse has a simple stomach but a greatly enlarged caecum and colon, and these organs are inhabited by micro-organisms with activities very similar to those of rumen organisms. Cellulose is digested and fatty acids are produced and absorbed, although the digestion of cellulose in roughages is less efficiently performed in the horse than in ruminants. Vitamins of the B complex are synthesised, but are not always produced or absorbed in quantities sufficient to meet requirements. Microbial digestion of soluble carbohydrates and of proteins and lipids is limited, because these are mainly digested and absorbed

before the digesta reach the caecum. In comparison with the ruminant the horse suffers from the disadvantage that the products of microbial digestion have less opportunity of being absorbed and no opportunity of being further broken down by its own digestive enzymes.

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Chapter 9

METABOLISM

Metabolism is the name given to the sequence or succession of chemical processes that take place in the living organism. Some of the processes involve the degradation of complex compounds to simpler materials and are designated by the general term *katabolism*. *Anabolism* describes those metabolic processes in which complex compounds are synthesised from simpler substances. Waste products arise as a result of metabolism, and these have to be transformed chemically and excreted; the reactions necessary for such transformations form part of the general metabolism. As a result of the various metabolic processes, energy becomes available for mechanical work, and for chemical work such as the synthesis of carbohydrates, proteins and lipids.

ENERGY METABOLISM

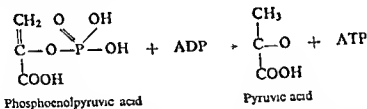
Energy may be defined as the capacity to do work. There are various forms of energy, such as chemical, heat, electrical and radiant, all of which are interconvertible by suitable means. Thus the radiant energy of the sun is utilised by green plants to produce complex plant constituents, and is stored as such. The plants are consumed by animals and the constituents broken down, releasing energy which is used by the animal for mechanical work, for syntheses and for providing heat under adverse climatic conditions.

Heat units are used to represent the various forms of energy involved in metabolism, since all forms of energy are convertible into heat. The basic unit is the calorie (cal), this being the quantity of heat required to raise the temperature of 1 g of water from 14.5 to 15.5° C. Electrical measurements are more accurately standardised, and the calorie is now officially defined as 4.1855 international joules. The calorie however is inconveniently small for use in nutrition, and the units usually employed are the kilocalorie (= 1,000 cal) and the megacalorie (= 1,000,000 cal). The former is abbreviated to kcal or, less preferably, to Cal, and the latter to Mcal.

The chemical reactions taking place in the animal body may be

endergonic and involve a gain of free energy by the system, or they may result in a loss of free energy from the system, in which case they are termed *exergonic*. Most of the synthetic reactions of the body are endergonic and require a supply of energy so that they may take place. This energy can be obtained from exergonic catabolic changes. Before the energy released by the exergonic reactions can be utilised for syntheses and other vital body processes, a connection between the two must be established. This is brought about by mediating compounds which take part in both processes, picking up energy from one and transferring it to the other.

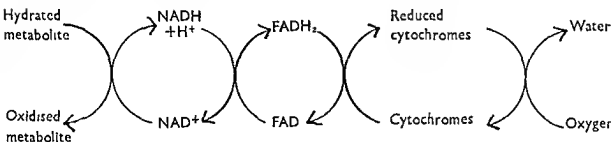
The most important mediating compound in the body is adenosine triphosphate (ATP). Adenosine is formed from the purine base, adenine, and the sugar, D ribose. Phosphorylation of the hydroxyl group at carbon atom 5 of the sugar gives adenosine monophosphate (AMP) (see Chapter 4), successive additions of phosphate residues give adenosine diphosphate (ADP), and then the triphosphate. The formation of these last two phosphate bonds requires a considerable amount of energy, which may be obtained directly by reaction of AMP or ADP with an energy rich material. Thus in carbohydrate breakdown, one of the steps is the change of phosphoenolpyruvic acid to pyruvic acid, which results in one molecule of ATP being produced from ADP.



Alternatively ATP may be produced indirectly. Most biological oxidations involve addition of water to a substrate and then removal of hydrogen, leaving an oxidised residue. The hydrogen released is removed as water, but the union with oxygen only occurs at the end of a series of reactions. A typical example is the removal of a hydrogen molecule via the NAD^+ pathway (see diagram at top of p. 125). The last three stages of the pathway are each accompanied by the release of sufficient energy for the synthesis of a mole of ATP from ADP and inorganic phosphate. Each mole of hydrogen so oxidised in the body yields three moles of ATP.

The energy fixed as ATP may be used for doing mechanical work in the performance of essential life processes in maintaining the animal,

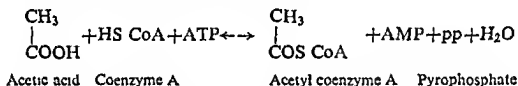
as in muscle contraction. This involves movement of the myosin and actin threads against each other, during which cross-linkages are broken and new ones formed. The formation of an actin-myosin-ATP



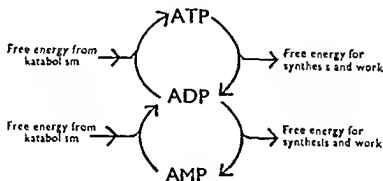
NAD⁺ Nicotinamide adenine dinucleotide
FAD Flavin adenine dinucleotide

complex is an intermediate in this process and breaks down giving myosin and actin again, but the ATP is broken down to ADP and inorganic phosphate. It is this breakdown which provides the energy required for contraction.

The energy fixed as ATP may also be used to drive synthetic reactions, as in the first stage of fatty acid synthesis.

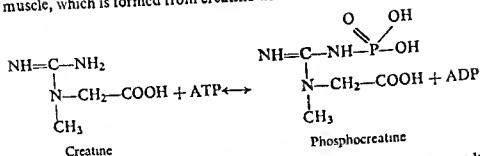


The role of ATP in the trapping and utilisation of energy is illustrated diagrammatically as follows:



Fixation of energy in the form of ATP is a transitory phenomenon, and any energy produced in excess of immediate requirements is stored in more permanent form in such compounds as the phosphocreatine of

muscle, which is formed from creatine when ATP is in excess



Then when the supply of ATP is insufficient to meet the demands for energy, more ATP is produced from phosphocreatine by the reverse reaction

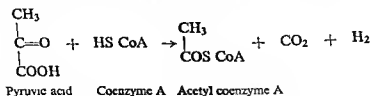
Even materials like phosphocreatine are only minor, temporary stores of energy—most energy is stored in the body as depot fat, and small quantities of carbohydrate in the form of glycogen. In addition, protein may be used to provide energy under certain circumstances.

As well as this stored energy, the body also derives energy directly from nutrients absorbed from the digestive tract. One of the chief of these is glucose.

Glucose as an Energy Source

Energy is released from glucose as the result of oxidation, which may take place in two ways. The most common is that proposed by Embden and Meyerhof, in which the first step is the breakdown of glucose to pyruvic acid, as shown in Fig 9.1. Two moles of ATP are used in the initial phosphorylations of stages 1 and 3, and the fructose diphosphate so formed then breaks down to give two moles of glyceraldehyde 3 phosphate. Subsequently an NAD^+ linked dehydrogenation at stage 7 yields three moles of ATP, and one mole of ATP is produced directly at each of stages 8 and 11. Ten moles of ATP are thus produced from one mole of glucose. Since two moles of ATP were used up, the net production of ATP from ADP is 8 moles per mole of glucose.

The pyruvic acid then undergoes oxidative decarboxylation by reaction with coenzyme A to give acetyl coenzyme A.



The hydrogen is removed via the normal NAD^+ pathway, yielding three moles of ATP from ADP. The acetylcoenzyme A is then oxidized to carbon dioxide and water via the tricarboxylic acid cycle, as shown in Fig. 9.2. This involves four dehydrogenations, two of which are

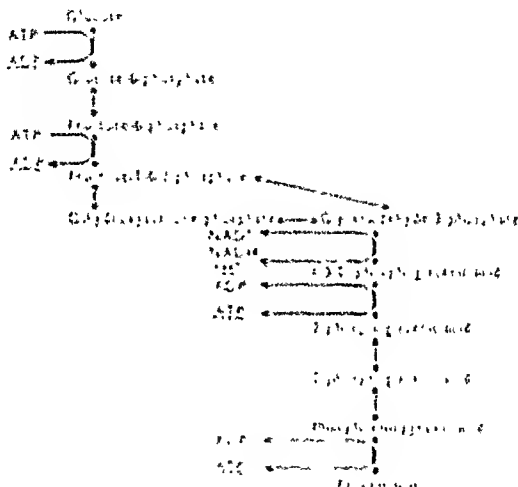


Fig. 9.2. Oxidation pathway of glucose to carbon dioxide.

The oxidation of glucose to carbon dioxide and water is a highly exothermic process. The energy released is used to drive the synthesis of ATP from ADP and inorganic phosphate. The energy released is also used to drive the synthesis of other biomolecules. The energy released is also used to drive the synthesis of other biomolecules. The energy released is also used to drive the synthesis of other biomolecules.

Energy released

Glucose	2870 kJ/mol
Pyruvate	1360 kJ/mol
Acetyl-CoA	1280 kJ/mol
CO ₂	394 kJ/mol
H ₂ O	286 kJ/mol

Thirty-eight phosphate bonds are formed, each of which yields approximately 12.5 kcal of energy when broken by hydrolysis under physiological conditions. Such phosphate bonds ($\sim P$) are commonly referred to as high energy bonds, although the term is not thermodynamically accurate. Each mole of glucose oxidised thus yields a total of 475 kcal of energy in utilisable form. The total free energy

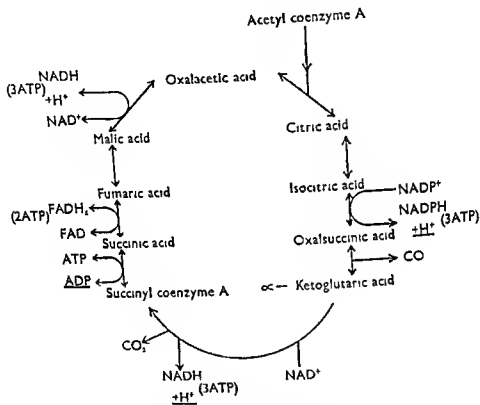


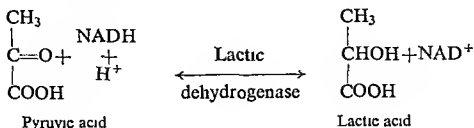
FIG 9.2 The tricarboxylic acid cycle

content of glucose at 37° C is 703 kcal per mole, and the efficiency of free energy capture by the body is

$$475/703 \times 100 = 67.5 \text{ per cent}$$

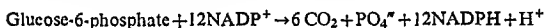
Under certain conditions there may be no oxygen available for the oxidation of hydrogen removed via the **NAD⁺** pathway. In order to allow the production of even a small amount of energy by the conversion of glucose to pyruvic acid, the reduced **NAD⁺** produced at stage 7 in Fig 9.1 must be converted to **NAD⁺** again. This takes

place by the formation of lactic acid from pyruvic acid in the presence of lactic dehydrogenase



A net production of two moles of ATP is then possible from each mole of glucose under adverse conditions such as prolonged intense muscular activity. The lactic acid may be transported to the liver, where it is converted into glucose and becomes available for further oxidation.

The second pathway of glucose oxidation in the body is the *hexose-phosphate shunt*. This involves addition of water to phosphorylated glucose followed by a series of NADP^+ linked dehydrogenations, and may be represented *in toto* as



The oxidation of hydrogen via the NADP^+ pathway yields thirty-six high-energy phosphate bonds. The initial phosphorylation of the glucose uses one mole of ATP, leaving a net production of thirty-five high-energy bonds per mole of glucose. The efficiency of free energy capture in this case is

$$437.5/703 \times 100 = 62.3 \text{ per cent}$$

The hexose-phosphate shunt is important in tissues where a supply of reduced NADP^+ rather than reduced NAD^+ is required.

Glycogen as an Energy Source

As well as being obtained directly from the digestive tract, glucose may become available for oxidation from the reserves of glycogen present in the body. Glucose 6-phosphate is produced by the action of inorganic phosphate and not ATP, so that energy production from glycogen is slightly more efficient than when glucose is the source.

Propionic Acid as an Energy Source

In ruminant animals considerable amounts of propionic acid become

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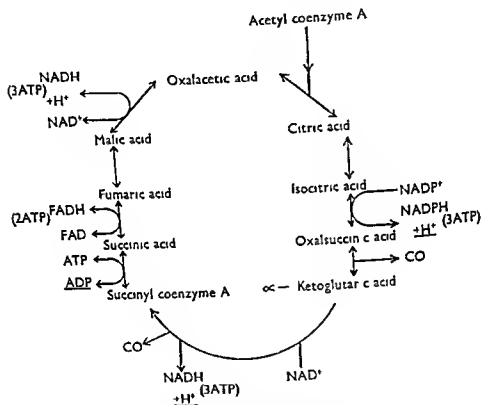


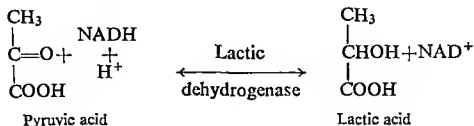
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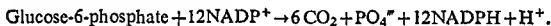
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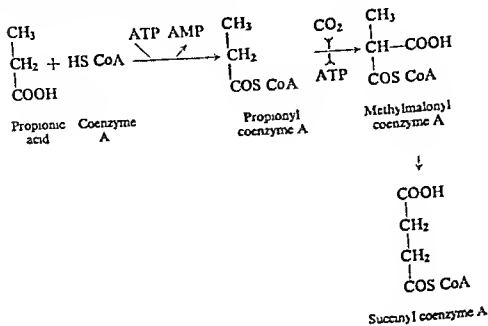
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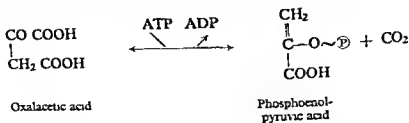
Propionic Acid as an Energy Source

In ruminant animals considerable amounts of propionic acid become

available to the body as a result of the fermentation of carbohydrate material in the rumen. The acid first undergoes reaction with coenzyme A to give propionyl coenzyme A, which is then changed to succinyl coenzyme A as follows



The succinyl coenzyme A may then enter the tricarboxylic acid cycle, where it is changed to oxalacetic acid with the production of six moles of ATP. The oxalacetic acid then gives phosphoenolpyruvic acid



This is then changed to acetyl coenzyme A, which is oxidised via the tricarboxylic acid cycle. The result is the formation of 18 moles of ATP from ADP per mole of propionic acid oxidised, i.e. the formation of 18 phosphate bonds each yielding approximately 12.5 kcal of energy on hydrolysis.

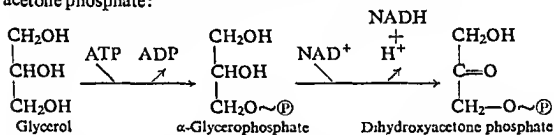
A balance sheet may be prepared as follows:

	Moles ATP	
	+	-
1 mole propionic acid to 1 mole oxalacetic acid	6	3
1 mole oxalacetic acid to 1 mole phosphoenolpyruvic acid		1
1 mole phosphoenolpyruvic acid to 1 mole acetyl coenzyme A	4	
1 mole acetyl coenzyme A to CO ₂ and H ₂ O	12	
	<hr/>	
Totals	22	4
Net gain per mole propionic acid	18	

Normally propionic acid produced in the rumen is transported to the liver and changed into glucose, which is then used as a source of ATP. The yield of ATP is again 18 moles ATP per mole of propionic acid oxidised.

Fat as an Energy Source

As a result of the hydrolysis of fat, glyccrol and fatty acids become available for energy production. The fatty acids are more important in this respect than the glycerol, which is first changed into dihydroxyacetone phosphate:

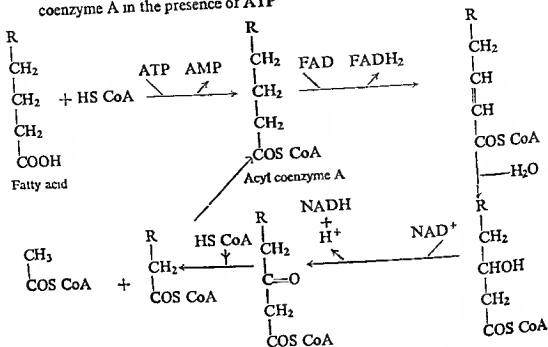


This is then converted to acetyl coenzyme A, which is oxidised to carbon dioxide and water via the tricarboxylic acid cycle. The net gain of ATP from ADP is 22 moles per mole of glycerol. This is shown in the following balance sheet:

	Moles ATP	
	+	-
1 mole glyccrol to 1 mole dihydroxyacetone phosphate	3	1
1 mole dihydroxyacetone phosphate to 1 mole acetyl coenzyme A	8	
1 mole acetyl coenzyme A to CO ₂ and H ₂ O	12	
	<hr/>	
Totals	23	1
Net gain per mole glycerol	22	

Fatty acids undergo a process of degradation known as β -oxidation, which results in a progressive shortening of the carbon chain by

removal of two carbon atoms at a time The first stage is reaction with coenzyme A in the presence of ATP

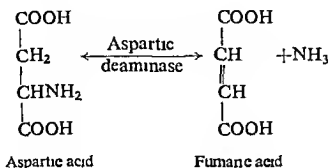


An acyl coenzyme A is thus produced which has two carbon atoms fewer than the original, and which can itself undergo further degradation in the same way. The process continues until the carbon chain has been changed completely to acetyl coenzyme A. This enters the tricarboxylic acid cycle and is oxidised to carbon dioxide and water, each mole giving twelve moles of ATP from ADP. Since the initial phosphorylation is only necessary once for each mole, more ATP is produced for the expenditure of the same amount of energy in the oxidation of a long-chain than a short chain acid. The six-carbon caproic acid would thus yield ten moles of ATP from reduced coenzymes arising during the production of three moles of acetyl coenzyme A. These, when oxidised via the tricarboxylic acid cycle, yield thirty six moles of ATP from ADP. The net gain of ATP, allowing for the two used in the initial phosphorylation, is 44 moles per mole of caproic acid oxidised, as shown below

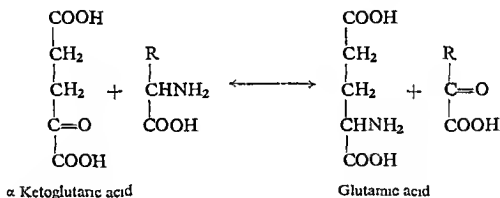
	Moles ATP	
	+	-
1 mole caproic acid to 3 moles acetyl coenzyme A	10	2
3 moles acetyl coenzyme A to CO ₂ and H ₂ O	36	
	<hr/>	
Totals	46	2
Net gain per mole caproic acid	44	

Amino Acids as an Energy Source

Amino acids in excess of the animal's requirements may be katabolised to give energy. The amino group is first removed by a process of deamination or transamination. Deamination is only extensive in the liver under the influence of specific deaminases, e.g.

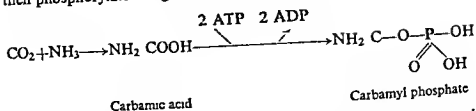


The majority of amino acids undergo transamination when they react with α -ketoglutaric acid to give a keto acid and glutamic acid, as follows

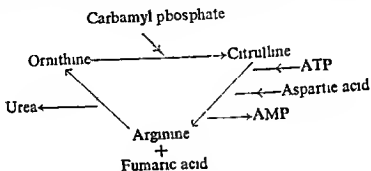


The glutamic acid is then deaminated by a specific deaminase to give ammonia and α ketoglutaric acid. Excess of glutamic acid derived from the food is similarly deaminated. The α -ketoglutaric acid may be used for further transamination, or may enter the tricarboxylic acid cycle and be oxidised to give oxalacetic acid and energy. The keto acids produced in the transamination reactions also enter the tricarboxylic acid cycle, being first changed to pyruvic acid or acetyl coenzyme A by a variety of pathways. The pyruvate and oxalacetate residues may also be converted into glucose. One of the consequences of amino acid katabolism is the production of ammonia, which has to be eliminated from the body. It is first changed into carbamic acid, which is

then phosphorylated to give carbamyl phosphate



This then reacts with ornithine to give citrulline, which reacts with further ammonia to give the amino acid, arginine. Ornithine and urea are then produced by hydrolysis. The reaction may be represented as follows



In assessing the efficiency of energy production the energy needed for urea synthesis must be set against that obtained by oxidation of the carbon residue of the amino acid. If we take glutamic acid as an example, this is first deaminated to α ketoglutaric acid, which enters the tricarboxylic acid cycle and is changed to oxalacetic acid, which in turn is changed to phosphoenolpyruvic acid, as shown on p 130. This is then oxidised to carbon dioxide and water via pyruvic acid, acetyl coenzyme A and the tricarboxylic acid cycle. The ammonia produced by deamination is eliminated as urea. A balance sheet may be prepared as follows

	Moles ATP	
	+	-
Deamination of 1 mole glutamic acid	3	
1 mole α ketoglutaric acid to oxalacetic acid	9	
1 mole oxalacetic acid to phosphoenolpyruvic acid		1
1 mole phosphoenolpyruvic acid to CO_2 and H_2O	16	
1 mole ammonia to carbamyl phosphate		2
1 mole citrulline to arginine		2
Totals	28	5
Net gain from 1 mole glutamic acid	23	

The efficiency as sources of energy of the nutrients discussed is summarised in Table 9.1.

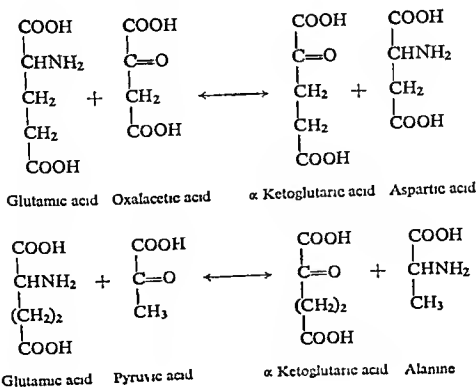
TABLE 9 1. Comparison of the Efficiency of certain Nutrients as Sources of Energy as ATP

<i>Nutrient</i>	<i>mole ATP/ mole nutrient</i>	<i>mole ATP/ 100 g nutrient</i>	<i>kcal heat of com- bustion per mole ATP produced</i>
Glucose	38	21.2 (4)	17.7 (1)
Propionic acid	18	24.3 (2)	20.4 (4)
Glycerol	22	23.9 (3)	18.0 (2)
Caproic acid	44	37.9 (1)	18.9 (3)
Acetic acid	10	16.7 (5)	20.9 (5)
Glutamic acid	23	15.6 (6)	—

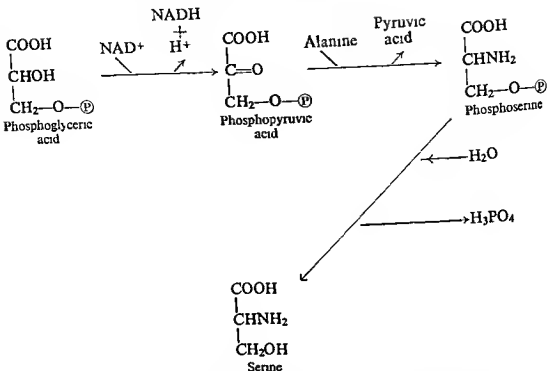
Figures in parenthesis denote order of efficiency

PROTEIN SYNTHESIS

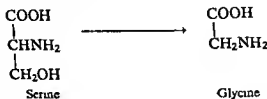
Proteins are synthesised from amino acids which become available either as the end-products of digestion or as a result of synthetic processes within the body. The latter may take place by transamination, as in the following examples



The alanine may then be used in making serine



Serine can then be changed to glycine by addition of water and removal of a formyl group by tetrahydrofolic acid (see p 68) together with an NADP^+ linked dehydrogenation



Amino acids may also be formed by reaction of keto acids with ammonium salts or urea, and arginine, as we have already seen, may be synthesised during urica formation

Not all amino acids, however, are capable of being synthesised in the body, and so they have to be supplied to the animal in the products of digestion, others are not synthesised at sufficient speed to satisfy the needs of the body, and these also have to be supplied to

the animal. Such amino acids are known as the Essential Amino Acids. The word 'essential' as used here does not mean that yet other amino acids are not required for the well-being of the animal, but simply that a supply of them is not necessary in the diet. All the twenty-five amino acids normally found in the body are physiological essentials; some ten or eleven are dietary essentials. As would be expected, the actual list of essential amino acids differs from species to species. In cattle and sheep, bacterial synthesis of amino acids in the rumen renders the inclusion of any specific amino acids in the diet unnecessary (see Chapter 13).

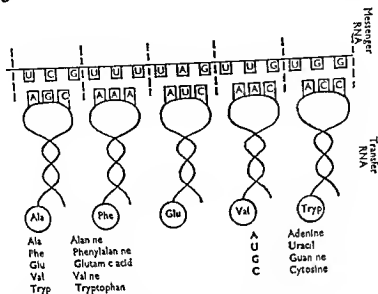
The amino acids absorbed into the blood stream from the gut are then transferred into the cells. This requires a supply of energy, since the concentration of amino acids in the cell may be up to one hundred times that in the blood and transfer into the cell has to take place against a very considerable concentration gradient. A continuous exchange takes place between the blood and cellular amino acids, but not between the free amino acids and those of the tissue proteins. The tissue proteins themselves undergo breakdown and resynthesis, the stability varying with different tissues. Thus liver protein has a half-life of seven days, while collagen on the other hand is so stable as to be considered almost completely inert.

The first step in protein synthesis is the enzymatic activation of the amino acids in the presence of ATP, to give complexes as follows:



Each amino acid has its own specific activating enzyme. In the activated state the amino acid combines with a molecule of transfer ribonucleic acid (RNA). Again, for each amino acid there is a specific transfer RNA which carries it to the ribosomes, where the amino acids are aligned at the surface of the messenger RNA. The transfer RNA molecule may be visualised as a hairpin, the legs being twisted around each other. The amino acid is attached to the free end of one of the legs. The head of the hairpin carries a sequence of nucleotides which determines the position it takes up on the messenger RNA. This in turn has a sequence of nucleotides which decides where each molecule of transfer RNA is attached. The actual active centre of the messenger RNA has a group of three out of four bases (see Chapter 4). The nature and order of the bases vary, and each corresponds to the base arrangement of the specific transfer RNA molecules. The actual code has been largely deciphered and the triplets of bases corresponding

to most amino acids are known, e.g. a triplet of three uracils codes for phenylalanine. We may thus envisage the amino acids held at the messenger RNA surface as follows:



The amino acids then join together by means of peptide linkages, and peel off as a polypeptide chain, as shown



The formation of each peptide bond requires the change of one mole of ATP to ADP. This is the primary form. The chain then becomes arranged in a secondary spiral form stabilised by hydrogen bonding. The tertiary structure involves extensive coiling and folding of the chain and is stabilised by hydrogen bonding, salt linkages and sulphur bridges. The quaternary structure involves polymerisation of the basic units.

The bases of the triplets of the messenger RNA are present as monophosphate, thought to be derived from base triphosphates. If this is so, then in the formation of one triplet, equivalent to one amino acid, the energy of six phosphate bonds is dissipated. Since the messenger RNA disintegrates after synthesis and has to be resynthesised for further protein formation, this expenditure of six bonds per amino

acid must be considered as part of the energy cost of protein synthesis.

The sequence of amino acids in a particular protein is determined by the structure of the messenger RNA. This is synthesised in the nucleus, where its structure is controlled by the deoxyribonucleic acid (DNA) of the nucleus. Protein structure is thus controlled ultimately by the inherited DNA of the nucleus.

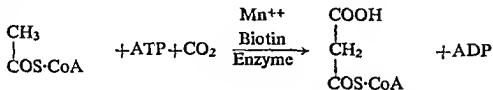
The mechanism of protein synthesis discussed does not involve addition of amino acids to an already formed peptide compound; all the amino acids are placed and joined simultaneously by condensation to form peptides. Unless all the amino acids required to synthesise the peptide are present at the right time, no synthesis takes place, and the amino acids which are present are then removed and katabolised. Considerable wastage of amino acids may take place if an incomplete mixture is presented for synthesis.

FAT SYNTHESIS

The glycerides of the depot fat may be derived from the glycerides of the blood, or from fatty acids and glycerol synthesised in the body.

Fatty acid synthesis

Until recently, fatty acid synthesis was visualised as taking place by the reverse of the well established β -oxidation pathway of fatty acid breakdown. A number of workers have now shown that the addition of two carbon compounds to the fatty acid chain is not a function of acetyl coenzyme A but of malonyl coenzyme A. The first stage is the transformation of acetyl coenzyme A to malonyl coenzyme A, as follows:

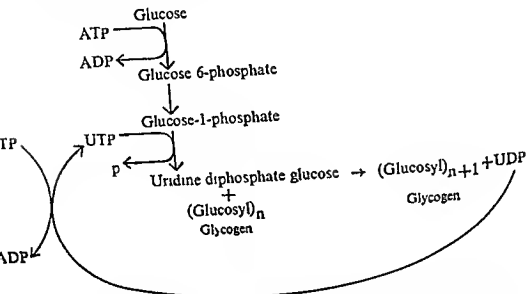


Acetyl coenzyme A

Malonyl coenzyme A

The malonyl coenzyme A reacts with a synthetase to give a malonyl enzyme complex, which then reacts with further acetyl coenzyme A

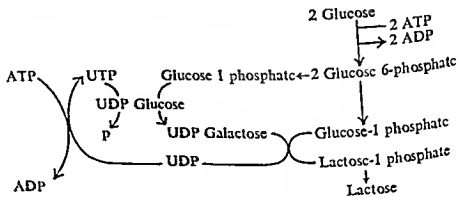
units when these are available in the body. The building up of the glycogen molecule requires the presence of uridine triphosphate (UTP) as a coenzyme. The process may be represented schematically as follows



When glycogen releases glucose, it does so by reaction with inorganic phosphate in the presence of a phosphorylase to give glucose-1-phosphate

Lactose Synthesis

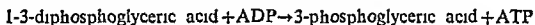
Lactose is a disaccharide formed by the condensation of one glucose and one galactose molecule. A supply of glucose is readily available, but the galactose has to be synthesised from the available glucose. This involves a configurational change at carbon atom 4 of the glucose. The synthesis may be represented schematically as follows



Estimates of the energetic efficiencies of the synthetic processes described are variable, since certain assumptions have to be made in the calculations. Generally carbohydrate synthesis is regarded as the most efficient at about 90-95 per cent, with protein synthesis and lipogenesis about 20 per cent less efficient, and lipogenesis the least efficient of the three.

CONTROL OF METABOLISM

The overall control of metabolism rests with the endocrine secretions such as thyroxine, which may raise or lower the metabolic rate in accordance with the amounts in which it is secreted. At a lower level a considerable degree of control is built into the metabolic pathways themselves. The rate of glucose breakdown via the Embden-Meyerhof pathway, for example, is controlled by the reaction

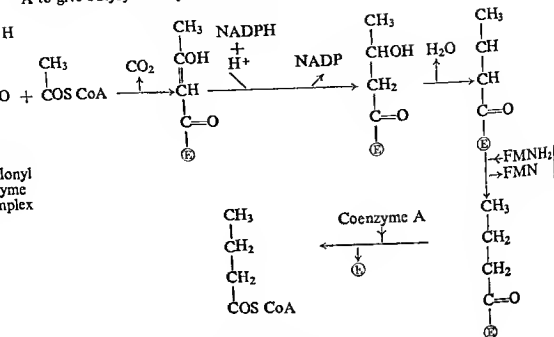


When ATP is being used up rapidly its breakdown ensures a plentiful supply of ADP and phosphoric acid, the reaction thus proceeds rapidly from left to right. If on the other hand ATP is not being used, the supply of ADP and inorganic phosphate is reduced and so is the speed of the reaction. The rate of glucose oxidation is thus tuned to the energy requirements of the body.

FURTHER READING

- K. L. BLAXTER, 1962 *The Energy Metabolism of Ruminants* Hutchinson, London
M. KLEIBER 1961 *The Fire of Life* John Wiley and Sons, New York
W. D. McELROY, 1961 *Cellular Physiology and Biochemistry* Prentice-Hall, New Jersey
H. N. MUNRO AND J. B. ALLISON (ed.), 1964 *Mammalian Protein Metabolism*, Vol I Academic Press, New York and London

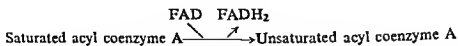
A to give butyryl coenzyme A, as follows



Butyryl coenzyme A

The butyryl coenzyme A then reacts with further malonyl coenzyme A, resulting in a lengthening of the chain by two carbon atoms to give caproyl coenzyme A. This in turn reacts with malonyl coenzyme A to give capryl coenzyme A. Such chain elongation does not take place indefinitely, but tends to stop when chain lengths of sixteen or eighteen carbon atoms are attained.

The coenzyme A derivatives of the saturated fatty acids may undergo an FAD linked dehydrogenation to give unsaturated acyl derivatives of coenzyme A, as follows

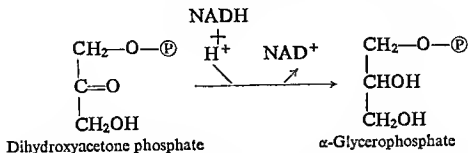


Only monoethenoid derivatives, such as oleic acid, are produced in this way. Diethenoid and triethenoid derivatives, like linoleic and linolenic acids, are not synthesised and must be supplied in the diet.

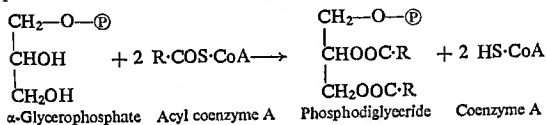
Glycerol Synthesis

Glycerol is synthesised in the body from glucose. The latter is first broken down via the Embden Meyerhof pathway to dihydroxyacetone

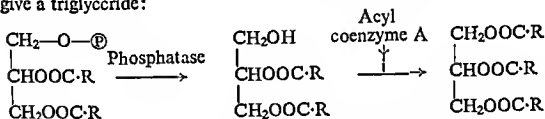
phosphate. This then undergoes reduction to α -glycerophosphate:



In this form glycerol may be esterified by the acyl coenzyme A molecules produced as above to give phosphodiglycerides:



The phosphate residue is then removed by the action of a phosphatase, and the diglyceride so formed reacts with another acyl coenzyme A to give a triglyceride:



Fats may be synthesised entirely from glucose, or they may be derived in part from acetic acid. It is interesting that in the mammary gland the hexose-phosphate shunt is the major pathway for glucose breakdown since it provides the reduced NADP^+ specifically required for fatty acid synthesis.

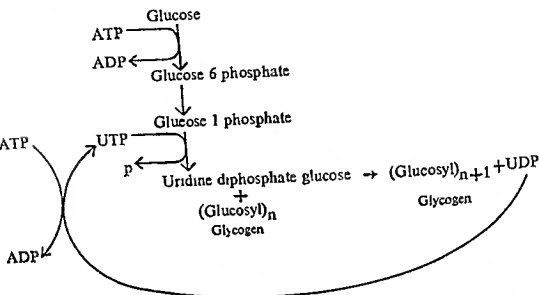
CARBOHYDRATE SYNTHESIS

The formation of glucose from simpler molecules such as propionic and keto acids has been discussed already. Glucose itself serves as the source material for the synthesis of two other important carbohydrates. These are the chief storage carbohydrate, glycogen, and milk sugar or lactose, the synthesis of which is specific to the mammary gland of the lactating animal.

Glycogen Synthesis

Glycogen is a complex polysaccharide made up of condensed glucose residues (Chapter 2), and has the ability to add on further glucose

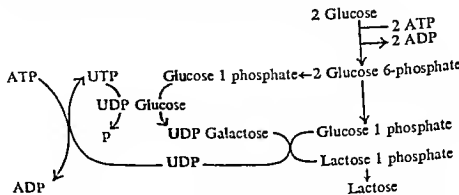
units when these are available in the body. The building up of the glycogen molecule requires the presence of uridine triphosphate (UTP) as a coenzyme. The process may be represented schematically as follows:



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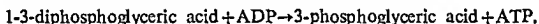
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H. N. MUNRO AND J. B. ALLISON (ed.), 1964. *Mammalian Protein Metabolism*, Vol I. Academic Press, New York and London.

THE EVALUATION OF FOODS

(A) DIGESTIBILITY

This chapter marks a change from qualitative to quantitative nutrition. Those preceding it have shown what substances are required by animals, how these substances are supplied in foods and the manner in which they are utilised. This chapter and those immediately following are concerned with the assessment, first, of the quantities in which nutrients are supplied by foods, and second, of the quantities in which they are required by different classes of farm animals.

The potential value of a food for supplying a particular nutrient can be determined by chemical analysis, but the actual value of the food to the animal can be arrived at only after making allowances for the inevitable losses that occur during digestion, absorption and metabolism. The first tax imposed on foods is that represented by the part of it which is not absorbed and is excreted in the faeces.

The digestibility of a food is most accurately defined as that proportion which is not excreted in the faeces and which is, therefore, assumed to be absorbed by the animal. It is commonly expressed in terms of dry matter and as a percentage, the digestibility coefficient. For example, if a cow ate 11 lb of hay containing 10 lb of dry matter and excreted 4 lb of dry matter in its faeces, the digestibility of the hay dry matter would be

$$\frac{10-4}{10} \times 100 = 60 \text{ per cent}$$

Coefficients could be calculated in the same way for each constituent of the dry matter. Although the proportion of the food not excreted in the faeces is commonly assumed to be equal to that which is absorbed from the digestive tract, there are objections to this assumption, which will be discussed later.

The Measurement of Digestibility

In a digestibility trial, the food under investigation is given to the animal in known amounts and the output of faeces measured. More

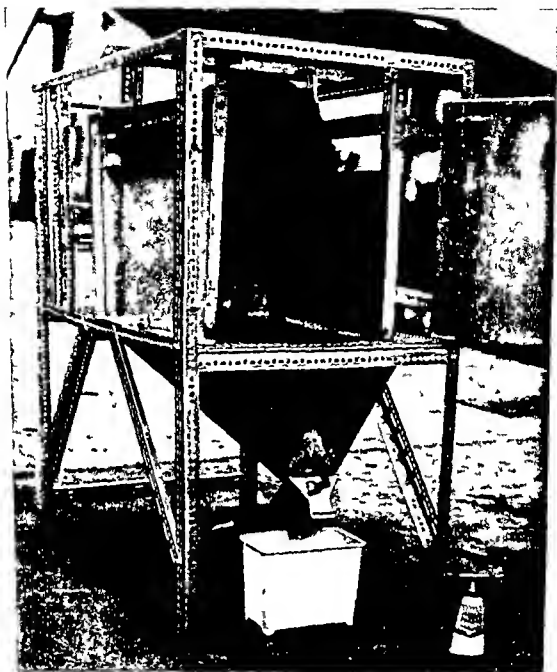


FIG. 10.1 Apparatus for the collection of faeces in digestibility trials
(a) Metabolism cage for sheep. Note wire mesh floor, collection chute and sieve (also shown on right) for separating faeces and urine. The former pass over the sieve into the front (dark-coloured) container. (By courtesy of the Rowett Research Institute.)



FIG 10 1 Apparatus for the collection of faeces in digestibility trials
 (a) Harness and bag for cattle. The weight of the rubber bag is transmitted mainly to the padded collar. With females urine is prevented from entering the bag by a diverting device fitted over the vulva. Neither method of collection causes the animal discomfort. (By courtesy of the Rowett Research Institute)

than one animal is used, firstly because animals, even when of the same species, age and sex, differ slightly in their digestive ability, and secondly because replication allows more opportunity for detecting errors of measurement.

In trials with mammals, male animals are preferred to females because it is easier to collect faeces and urine separately with the male. They should be docile and in good health. Small animals are confined in metabolism cages (Fig. 10.1a) which separate faeces and urine by an arrangement of sieves, but larger animals such as cattle are fitted with harness and faeces collection bags made of rubber or of a similar impervious material (Fig. 10.1b). For females a special device channels faeces into the bag while diverting urine. Similar equipment can be used for sheep.

For poultry, the determination of digestibility is complicated by the fact that faeces and urine are voided from a single orifice, the cloaca. The compounds present in urine are mainly nitrogenous, and faeces and urine can be separated chemically if the nitrogenous compounds of urine can be separated from those of faeces. The separation is based either on the fact that most urine nitrogen is in the form of uric acid or that most faecal nitrogen is present as true protein. It is also possible to alter the fowl's anatomy by surgery so that faeces and urine are voided separately.

The food required for the trial should if possible be thoroughly mixed beforehand, to obtain uniform composition. It is then given to the animals for at least a week before collection of faeces begins, in order to accustom the animals to the diet and to clear from the tract the residues of previous foods. This preliminary period is followed by a period when food intake and faecal output are recorded. This experimental period is usually 5 to 14 days long, with longer periods giving greater accuracy. With simple-stomached animals the faeces resulting from a particular input of food can be identified by adding an indigestible coloured substance such as ferric oxide or carmine to the first and last meals of the experimental period; the beginning and the end of faecal collection are then delayed until the dye appears in and disappears from the excreta. With ruminants this method is not successful because the dyed meal mixes with others in the rumen, and instead an arbitrary time-lag of 24 to 48 hours is normally allowed for the passage of food residues, i.e. the measurement of faecal output begins 1 to 2 days after that of food intake.

In all digestibility trials, and particularly those with ruminants, it is highly desirable that meals should be given at the same time each

day and that the amounts of food eaten should not vary from day to day. When intake is irregular there is the possibility, for example, that if the last meal of the experimental period is unusually large the subsequent increase in faecal output may be delayed until after the end of faecal collection. In this situation the output of faeces resulting from the measured intake of food will be underestimated and digestibility overestimated. The trial is completed by analysing samples of the food used and the faeces collected.

Table 10.1 gives an example of a digestibility trial in which sheep

TABLE 10.1. Results of a Digestibility Trial in which Three Sheep were Fed on Hay

1. The average quantity of hay dry matter eaten was 1.63 kg per head per day, and the average quantity of dry matter excreted in the faeces was 0.76 kg per head per day. Hay and faeces were analysed, with the following results (percentage of dry matter):

	<i>Organic matter</i>	<i>Crude protein</i>	<i>Ether extract</i>	<i>Crude fibre</i>	<i>N-free extractives</i>
Hay	91.9	9.3	1.5	35.0	46.1
Faeces	87.0	11.0	1.5	31.7	42.8

2. From these figures the quantities of the dry matter and its components which were consumed, excreted and, by difference, digested were calculated as follows (kg):

	<i>Dry matter</i>	<i>Organic matter</i>	<i>Crude protein</i>	<i>Ether extract</i>	<i>Crude fibre</i>	<i>N-free extractives</i>
Consumed	1.63	1.50	0.15	0.02	0.57	0.75
Excreted	0.76	0.66	0.08	0.01	0.24	0.33
Digested	0.87	0.84	0.07	0.01	0.33	0.42

3. The digestibility coefficients were calculated by expressing the weights digested as percentages of the weights consumed:

	<i>Dry matter</i>	<i>Organic matter</i>	<i>Crude protein</i>	<i>Ether extract</i>	<i>Crude fibre</i>	<i>N-free extractives</i>
	53.4	56.0	46.7	50.0	57.9	56.0

4. Finally, the composition of the hay was calculated in terms of digestible nutrients with the following results:

	<i>Digestible organic matter</i>	<i>Digestible crude protein</i>	<i>Digestible ether extract</i>	<i>Digestible crude fibre</i>	<i>Digestible N-free extractives</i>
	51.5	4.3	0.8	20.3	25.8

were fed on hay for a preliminary period of ten days and an experimental period of ten days. The results for three animals have been combined as averages.

In this example the food in question was roughage and could be given to the animals as the sole item of diet. Concentrated foods, however, are not normally given alone to ruminants because they cause digestive upsets, and their digestibility must be determined by giving them in combination with a roughage of known digestibility. Thus the hay of the example could have been used in a second trial in which the sheep also received 0.5 kg of oats per day. If the dry matter content of the oats was 90 per cent., daily dry matter intake would increase by 0.45 kg, and if the output of faecal dry matter increased by 0.15 kg the digestibility of the dry matter in oats would be calculated as

$$\frac{0.45 - 0.15}{0.45} \times 100 = 67 \text{ per cent.}$$

Special Methods for Measuring Digestibility

Indicator methods. In some circumstances the lack of suitable equipment or the particular nature of the trial may make it impracticable to measure directly either food intake or faeces output, or both. For instance, when animals are fed as a group it is impossible to measure the intake of each individual. Digestibility can still be measured, however, if there is present in the food some substance which is known to be completely indigestible. If the concentrations of this indicator substance in the food and in small samples of the faeces of each animal are then determined, the ratio between these concentrations gives an estimate of digestibility. For example, if the concentration of the indicator increased from 1 per cent. in the food dry matter to 2 per cent. in the faeces, this would mean that 50 per cent. of the dry matter had been digested and absorbed. In equation form,

Digestibility

$$= \frac{\text{per cent. indicator in faeces} - \text{per cent. indicator in food}}{\text{per cent. indicator in faeces}} \times 100.$$

The indicator may be a natural constituent of the food or be added to it. Lignin is used as a natural indicator, and the substance most commonly added is chromic oxide, Cr_2O_3 .

Measuring the digestibility of the herbage eaten by grazing animals presents a particularly difficult problem. It might appear that lignin

could be used as an indicator, but it is extremely difficult to determine the lignin content of the herbage eaten by grazing animals. The reason is that animals graze selectively, preferring young plants to old, and leaf to stem, and the herbage they actually consume usually has a lignin content lower than that of a cut sample of herbage. This means that estimates of digestibility must be based entirely on the composition of the faeces. Fortunately there is a close positive relationship between herbage digestibility and the concentration of nitrogen in faeces, which permits digestibility to be estimated by determining the nitrogen concentrations of small samples of faeces.

Laboratory methods of estimating digestibility Since digestibility trials are laborious to perform, there have been numerous attempts made to determine the digestibility of foods by reproducing in the laboratory the reactions which take place in the alimentary tract of the animal. Digestion in non ruminants is not easily simulated in its entirety, but the digestibility of food protein may be determined from its susceptibility to attack *in vitro* by pepsin and hydrochloric acid. The microbial digestion occurring in ruminants can be reproduced in the laboratory by incubating a sample of the food with rumen liquor in an 'artificial rumen'.

The artificial rumen, which is used to study qualitative as well as quantitative aspects of digestion, has as its essential features a glass vessel and arrangements to ensure anaerobiosis and a uniform pH. In more elaborate models the dynamic state of the living rumen is reproduced by dialysing out the products of digestion and by adding 'artificial saliva'. The *in vitro* digestibility coefficient is determined as the proportion of the food brought into solution during incubation. Ideally it should be equal to the *in vivo* coefficient, but usually it is smaller and a correction factor must be used to predict the coefficient applying in the animal.

The artificial rumen is particularly useful for obtaining approximate digestibility values for a large number of samples, as in the analysis of farm roughages for advisory purposes, and for determining the digestibility of small samples such as those available to the plant breeder.

The Validity of Digestibility Coefficients

The assumption that the proportion of food digested and absorbed can be determined by subtracting the part excreted in the faeces is open to question on two counts. The first is that in ruminants the methane arising from the fermentation of carbohydrates is lost by eructation,

and not absorbed. This loss leads to overestimation of the digestible carbohydrate and digestible energy content of ruminant foods.

More serious errors are introduced by the fact that, as discussed in Chapter 8, not all the faeces are actual undigested food residues. Part of the faecal material is contributed by enzymes and other substances secreted into the gut and not reabsorbed, and by cellular material abraded from the lining of the gut. Thus if an animal is fed on a nitrogen-free diet it continues to excrete nitrogen in the faeces. Since this nitrogen is derived from the body and not directly from the food, it is known as the metabolic faecal nitrogen; the amounts in which it is excreted are approximately proportional to the animal's dry matter intake. Faeces also contain appreciable quantities of ether-extractable substances which are of metabolic origin. Some of the ash fraction of faeces is contributed by mineral elements secreted into the gut, because the faeces serve as the route of true excretion of certain minerals, particularly calcium.

The excretion in faeces of substances not arising directly from the food leads to underestimation of the proportion of the food actually absorbed by the animal. The values obtained in digestibility trials are therefore called *apparent digestibility coefficients* to distinguish them from the coefficients of true digestibility. In practice the latter are difficult to determine, because the fractions of the faeces attributable to the food and to the animal are in most cases indistinguishable from one another. Apparent coefficients are satisfactory for organic constituents of foods, and they do represent the net result of the ingestion of food. Apparent coefficients for mineral elements, however, are often meaningless, because they depend so much on the animal's need for a particular element. If a digestibility trial follows a period when large amounts of calcium have been stored, for example, the animal may excrete more calcium in the faeces than it ingests in the food, and a negative coefficient will result.

Factors Affecting Digestibility

Food composition. The digestibility of a food is closely related to its chemical composition, and a food like barley, which varies relatively little in composition from one sample to another, will show little variation in digestibility. Other foods however, particularly fresh or conserved herbages, are much less constant in composition and therefore vary more in digestibility. The crude fibre fraction of a food has the greatest influence on its digestibility, and both the amount and chemical composition of the crude fibre are important. Pure cellulose

is readily digested by ruminants and even by some non-ruminants (see Chapter 8), but if much lignin is associated with the cellulose, the digestibility of the crude fibre fraction is reduced accordingly. An increase in the proportion of crude fibre in a particular food, such as occurs in maturing pasture herbage, is generally accompanied by greater lignification of the cell walls. The consequent reduction in crude fibre digestibility inevitably lowers the digestibility of other constituents, since unbroken cell walls prevent the access of digestive enzymes to the cell contents. Thus an increase in the crude fibre content of many foods by one percentage unit causes a reduction in the digestibility of the total organic nutrients of 0.7 to 1.0 unit for ruminants and of twice this value for pigs.

The apparent digestibility of crude protein is particularly dependent upon the proportion of protein in the food. The reason for this is that the metabolic faecal nitrogen represents a constant tax upon dietary nitrogen and protein. In ruminants the output of metabolic faecal nitrogen is equivalent to about 3 g of crude protein per 100 g of food dry matter eaten. If the food contains 6 per cent crude protein (i.e. 6 g per 100 g of dry matter), the apparent digestibility of this protein cannot be greater than 50 per cent, but if the food contains 12 per cent, the effect of the metabolic faecal nitrogen is relatively smaller and the maximum possible apparent digestibility of the food protein rises to 75 per cent. A consequence of this effect is that foods containing less than 3 per cent of crude protein, such as cereal straws, may actually reduce the digestible protein supply of the animal.

Ration composition The digestibility of a food is influenced not only by its own composition, but also by the composition of other foods consumed with it. This *associative* effect of foods represents a serious objection to the determination of the digestibility of concentrates by difference as described on page 147. For example, a sample of barley might differ in digestibility according to whether it were eaten with hay or with silage, or barley given with hay might alter the digestibility of the roughage itself. This effect is partly explained by recently acquired knowledge of digestion in the rumen. In Chapter 8 it was mentioned that the extent of digestion in the rumen depends very much on the balance of nutrients and that, for example, an excess of soluble carbohydrates in the diet will depress the digestion of cellulose.

Preparation of foods The commonest treatments applied to foods are chopping, chaffing, crushing or grinding, and cooking. In order to obtain maximum digestibility cereal grains should be crushed for cattle and ground for pigs, otherwise they may pass through the gut intact.

The chaffing of roughages has little effect on digestibility, but if applied to materials of poor quality, such as the cereal straws, it will prevent the animal from selecting the palatable and more digestible parts. The grinding of roughages often depresses their digestibility by increasing the rate at which they pass through the gut. Cooking does little to improve digestibility, except in the case of maize and potatoes given to pigs and poultry.

Animal factors Digestibility is more a property of the food than of the consumer, but this is not to say that a food given to different animals will always be digested to the same extent. The most important animal factor is the species of the consumer. Foods low in fibre are equally well digested by ruminants and non ruminants, but more fibrous foods are better digested by ruminants. Apparent digestibility coefficients for proteins are frequently higher for pigs because their excretion of metabolic faecal nitrogen is smaller than that of ruminants. Differences between the digestive abilities of sheep and cattle are small and of no practical importance. The age of the animal has little effect in non-ruminants, nor in ruminants once they have acquired a normal rumen flora.

Level of feeding An increase in the quantity of a food eaten by an animal causes a faster rate of passage of digesta. The food is then exposed to the action of digestive enzymes for a shorter period, so that there may be a reduction in its digestibility. This level of feeding effect is a complex one, and its magnitude depends particularly on the nature of the food. The dry matter digestibility of fresh or conserved grass is reduced only by 1 to 3 units when intake is increased by 50 to 100 per cent. For concentrates the effect is more complicated, because they are eaten by ruminants with a roughage. If roughage and concentrate are increased in equal proportions, and the composition of the diet is unchanged, the magnitude of the level of feeding effect is the same as for roughages alone. If on the other hand concentrate intake alone is increased, the composition of the diet changes and the reduction in its digestibility is greater. The effect may then be due partly to the associative effect of foods, discussed above.

The Total Digestible Nutrients System for Evaluating Foods

Tables giving the proximate composition of foods generally include values for digestible composition. It should now be clear that the latter values are average figures, not biological constants, and may be inaccurate when applied to a particular sample of food given to a particular animal. Average digestibility coefficients must therefore be

used with caution, especially when the food in question is one which may show considerable variations in composition. Digestibility data are important nevertheless, for the digestible composition of foods is used in several systems of food evaluation as a basis for calculating their energy supplying power. The Starch Equivalent system used in Europe will be described in Chapter 12, in the United States and a number of other countries foods are evaluated in terms of their Total Digestible Nutrients (TDN). In this system a value is calculated for each food as follows

$$\text{TDN} = \text{per cent. dig. crude protein} + \text{per cent. dig. crude fibre} \\ + \text{per cent. dig. NFE} + 2.25 (\text{per cent. dig. ether extract})$$

Thus the hay quoted in Table 10.1 would have a TDN value of 52.2

The ether extract is multiplied by 2.25 because the energy value of fats is approximately two and a quarter times as great as that of carbohydrates. The TDN system has not been used in the United Kingdom except in the feeding of pigs. In comparison with other systems of expressing energy value it has the merit of simplicity. Its disadvantage is that it fails to take into account that the efficiency with which the digested energy yielding nutrients are metabolised and made available to the animal varies from one food to another.

The Availability of Mineral Elements

As mentioned above the faeces serve as the route for true excretion of certain minerals, particularly calcium, phosphorus, magnesium and iron, and apparent digestibility coefficients for these thus have little significance. The measure of importance is therefore true digestibility, which for minerals is commonly called 'availability'. To measure the availability of a mineral one must generally distinguish between the portion in the faeces which represents unabsorbed material and the portion which represents material discharged into the gut from the tissues. In recent years this distinction has been made by labelling an element within the body, and hence the portion secreted into the gut, with a radioactive isotope.

In considering the factors which affect availability one needs to start with attributes of the animal, for the generalisation made earlier, that digestibility is a feature more of the food than of the animal consuming it, is not applicable to mineral availability. Firstly, mineral availability, like that of organic nutrients, varies with the species of animal. An outstanding example of a species difference in this respect, which has

been referred to earlier, is the superiority of ruminant over non-ruminant species in their ability to utilise phytate phosphorus. But the major feature of the animal which influences availability is undoubtedly age. For calcium, phosphorus and magnesium it has been shown that, while availability is often close to 100 per cent. in young animals, it falls steadily with increasing age until values at maturity may be less than 50 per cent. for calcium and even as low as 20 per cent. for magnesium. In part this decline is brought about by the inevitable changes in diet experienced by animals as they age, availability being generally high for milk and milk products.

Differences between foods in the availability of minerals are often due to interactions among the elements themselves or between minerals and other constituents of the diet. These interactions have been discussed previously in Chapter 8. The classic example is the dependence of calcium and phosphorus absorption on the relative proportions of the two elements in the food and on the vitamin D status of the animal.

While no attempt is made here or in Chapter 8 to provide a complete list of the factors which influence the availability of minerals, those mentioned serve to illustrate why no attempt is made in tables of feed composition to give values for availability comparable to the digestibility coefficients commonly quoted for organic nutrients. Because the availability of the minerals in a particular food depends so much on the other constituents of the diet and on the animal to which it is given, average values for availability would be of little significance.

Digestibility and Food Consumption in Ruminant Animals

The diet of ruminants commonly contains a high proportion of the bulky foods known collectively as roughages, and indeed may consist of them entirely. Roughages range in dry matter digestibility from over 80 per cent. for fresh pasture herbage to less than 40 per cent. for cereal straws. Those at the lower end of this range are dilute sources of digestible nutrients, and the animal consuming them has to pass large quantities through its digestive tract in order to satisfy its nutrient requirements. While the ruminant has a large capacity for food, the quantities it can consume may still be limited by the rate at which it can break down and remove food from its digestive tract.

The rate of removal depends on two processes: the absorption of the digestible constituents of the food, and the passage of the indigestible constituents through the tract and their expulsion in the faeces. While the whole of the digestive tract is concerned with these processes, it is

believed that the overall rate of removal is determined in most instances by the rate at which digesta are cleared from the rumen.

The properties of a food which determine the *rate* at which it is digested are basically the same as those which determine the *extent* to which it is digested. Fibrous foods of low digestibility are broken down slowly, because in the first instance the rate at which physical comminution can take place is low. Apart from delaying the access of

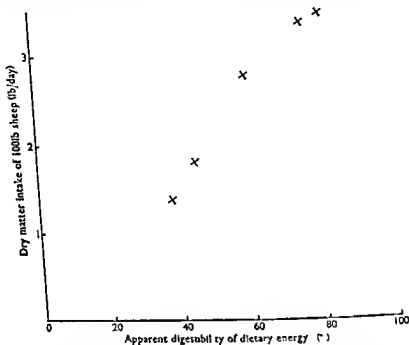


FIG 10.2 Food consumption and digestibility in sheep fed on roughages (After K. L. Blaxter, F. W. Wainman and R. S. Wilson 1961 *Anim. Prod.* 3: 51)

enzymes to the food constituents, slower physical breakdown leads to a more lengthy retention of food in the rumen, for only particles of small size are permitted to pass on down the tract. Chemical digestion in the rumen is retarded by the larger quantities of cellulose in fibrous foods, since cellulose is digested relatively slowly. There is, then, a relation between digestibility and rate of digestion which leads in turn to a relation between digestibility and food consumption. The nature of the latter relationship is made clear by considering the case of an animal being allowed to eat roughage to appetite at discrete meals. The more digestible the food is and the faster it is removed from the rumen, the greater will be the space cleared in the rumen in the interval between

meals, and the more the animal will be able to eat. (This effect of digestibility on food intake should not be confused with the effect of intake on digestibility mentioned previously, whereby reducing the amount of food given causes a small increase in its digestibility.)

An example of the relationship between digestibility and food consumption is shown in Fig. 10.2, which relates to sheep given various roughages to appetite as their sole item of diet. Digestibility here is expressed as the coefficient for food energy (see Chapter 11), but the percentages approximate to those for dry matter. Sheep given solely oat hay, 40 per cent. digestible, ate less than half as much dry matter as when they were given dried grass, 74 per cent. digestible. The difference in *digestible* dry matter intake is, of course, much greater, intake from the dried grass being four times as great.

This relationship between digestibility and food consumption in ruminants is a general one, and it may be modified by the influence on intake of properties of foods other than digestibility. If roughages are finely ground, for example, their digestibility is reduced but their consumption is increased, both effects being attributable to the faster rate at which the fine particles leave the rumen and pass on down the gut. When a diet of roughage is supplemented with a concentrate, the increase in total food intake which generally takes place is often greater than can be accounted for by the higher digestibility of the supplemented diet. For highly digestible roughages, differences in digestibility may have a relatively smaller effect on intake than for less digestible materials (as Fig. 10.2 suggests). Indeed it is possible that, when high levels of digestibility are attained, food consumption in ruminants is no longer limited by the rate at which digesta can be removed from the tract, but is controlled in the manner of non-ruminants (Chapter 14). The latter respond to improvements in the concentration of digestible nutrients in their diet by eating less food, not more, and thus maintain digestible nutrient intake at an approximately constant level.

FURTHER READING

- B. H. SCHNEIDER, 1947. *Feeds of the World, their Digestibility and Composition*. Agric. Exp. Sta., West Virginia University, U.S.A.
K. L. BLAXTER, 1962. *The Energy Metabolism of Ruminants*. Hutchinson, London.

THE EVALUATION OF FOODS

(B) THE ENERGY CONTENT OF FOODS AND THE PARTITION OF FOOD ENERGY WITHIN THE ANIMAL

The major organic nutrients are required by animals as materials for the construction of body tissues and the synthesis of such products as milk and eggs, and they are needed also as sources of energy for work done by the animal. A unifying feature of these diverse functions is that they all involve a transfer of energy, and this applies both when chemical energy is converted into mechanical or heat energy, as when nutrients are oxidised, and when chemical energy is converted from one form to another, as for example when body fat is synthesised from food carbohydrate. The ability of a food to supply energy is therefore of great importance in determining its nutritive value. The purpose of this chapter and the next is to discuss the fate of food energy in the animal body, the measurement of energy metabolism and the expression of the energy value of foods.

THE DEMAND FOR ENERGY

An animal deprived of food continues to require energy for those functions of the body immediately necessary for life—for the mechanical work of essential muscular activity, for chemical work such as the movement of dissolved substances against concentration gradients, and for the synthesis of expended body constituents such as enzymes and hormones. In the starving animal the energy required for these purposes is obtained by the catabolism of the body's reserves, first of glycogen, then of fat and protein. In the fed animal the primary demand on the energy of the food is in meeting this requirement for *body maintenance* and so preventing the catabolism of the animal's tissues.

When the chemical energy of the food is used for the muscular and chemical work involved in maintenance, the animal does no work on its surroundings and the energy used is converted into heat. Energy so used is regarded as having been expended, since heat energy is useful to the animal only in maintaining body temperature. In a fasting

animal the quantity of heat produced is equal to the quantity of chemical energy expended for body maintenance, and when measured under specific conditions is known as the animal's *basal metabolism*. In Chapter 14 it will be shown how estimates of basal metabolism are used in assessing the maintenance energy requirements of animals.

Energy supplied by the food in excess of that needed for maintenance is used for the various forms of production (More correctly, the nutrients represented by this energy are so used.) A young growing animal will store energy principally in the protein of its new tissues, a fattening animal stores energy in fat, and a lactating animal will transfer food energy into the energy contained in milk constituents. Some other forms of production are the performance of muscular work and the formation of wool and eggs. No function, not even body maintenance, can be said to have absolute priority for food energy. A young animal receiving adequate protein but insufficient energy for maintenance may still store protein while drawing on its reserves of fat. Similarly, some wool growth continues to take place in animals with sub-maintenance intakes of energy, and even in fasted animals.

THE SUPPLY OF ENERGY

The Gross Energy of Foods

The animal obtains energy from its food. The quantity of chemical energy present in a food is measured by converting it into heat energy, and determining the heat produced. This conversion is carried out by oxidising the food by burning it, the quantity of heat resulting from the complete oxidation of unit weight of a food is known as the *gross energy* or *heat of combustion* of that food.

Gross energy is measured in an apparatus known as a bomb calorimeter, which in its simplest form consists of a strong metal chamber (the bomb) resting in an insulated tank of water. The food sample is placed in the bomb, and oxygen admitted under pressure. The temperature of the water is taken, and the sample is then ignited electrically. The heat produced by the oxidation is absorbed by the bomb and the surrounding water, and when equilibrium is reached the temperature of the water is taken again. The quantity of heat produced is then calculated from the rise in temperature and the weights and specific heats of the water and the bomb.

The bomb calorimeter can be used to determine the gross energy of whole foods or of their constituents. It is also used for animal tissues and for the excretory products of animals. Some typical gross energy

values are shown in Table 11.1. Fats contain about two and a half times as much energy as carbohydrates, the difference reflecting the larger ratio of carbon *plus* hydrogen to oxygen in the former (i.e. fats are in a lower state of oxidation and are, therefore, capable of yielding more energy when oxidised). Proteins also have a higher gross energy value than carbohydrates. In spite of these differences among food

TABLE 11.1 Some typical Gross Energy Values
(kcal per g of dry matter)

<i>Animal tissues</i>	
Beef muscle (ash free)	5.32
Beef fat (ash free)	9.37
<i>Food constituents</i>	
Glucose	3.74
Starch	4.23
Cellulose	4.18
Casein	5.86
Butterfat	9.21
Fat (from oily seeds)	9.33
<i>Foods</i>	
Maize	4.43
Oats	4.68
Oat straw	4.43
Linseed oil meal	5.12
Grass hay	4.51
Milk (containing 4 per cent fat and 12.6 per cent total solids)	5.95

constituents, the predominance of the carbohydrates means that the foods of farm animals vary little in gross energy content. Only foods rich in fat such as linseed oil meal with 9 per cent ether extract, have high values and only those rich in ash, which has no caloric value, are much lower than average. Most common foods contain about 4.4 kcal per g or 2000 kcal per lb of dry matter.

Digestible Energy

The gross energy value of a food is an inaccurate estimate of the energy actually available to the animal because it fails to take into account the losses of energy occurring during digestion and metabolism. The first source of loss to be considered is that of the energy contained in the faeces. The *apparently digestible energy* of a food is the gross energy less the energy contained in the faeces which result from any particular input of that food.

In the example of a digestibility trial given in Table 10.1, the sheep

ate 1.63 kg of hay dry matter having an energy content of 4.30 kcal per g. Total energy intake was therefore 7009 kcal per day. The 0.76 kg of faeces dry matter contained 4.48 kcal per g, or a total of 3405 kcal, per day. The apparent digestibility of the energy of the hay was therefore $\frac{7009 - 3405}{7009} \times 100$ or 51.4 per cent., and the digestible energy content of the hay dry matter was $\frac{51.4}{100} \times 4.30 = 2.21$ kcal per g (1003 kcal per lb).

Metabolisable Energy

The animal suffers further losses of energy-containing substances in its urine and, if a ruminant, in the combustible gases leaving the digestive tract. The *metabolisable energy* of a food is the digestible energy less the energy lost in urine and combustible gases. The energy of urine is present in nitrogen-containing substances such as urea, hippuric acid, creatinine and allantoin, and also in such non-nitrogenous compounds as glucuronates and citric acid.

The combustible gases lost from the rumen consist almost entirely of methane. Methane production is closely related to food intake, and at the maintenance level of nutrition about 8 per cent. of the gross energy of the food is lost as methane. At higher levels of feeding the proportion falls to 6 or 7 per cent.

The metabolisable energy value of a food is determined in a feeding trial similar to a digestibility trial, but in which urine and methane, as well as faeces, are collected. Metabolism cages for sheep and pigs incorporate a device for collecting urine. The urine of cattle is caught in rubber urinals attached below the abdomen for males and over the vulva for females, and is piped by gravity or suction to a collection vessel. When methane production is measured the animal must be kept in an airtight container known as a respiration chamber. The operation of such chambers is described in more detail later (p. 167).

When no respiration chamber is available, methane production can be estimated as 8 per cent. of gross energy intake. In addition, it is possible to estimate the metabolisable energy values of ruminant foods from digestible energy values by multiplying by 0.8. This implies that, on average, about 20 per cent. of the energy apparently digested is excreted in the urine and as methane.

Factors affecting the metabolisable energy values of foods. Table 11.2 shows metabolisable energy values for a number of foods. It is clear that, of the sources of energy loss so far considered, the faecal loss is

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Factors affecting the metabolisable energy values of foods. Table 11.2 shows metabolisable energy values for a number of foods. It is clear that, of the sources of energy loss so far considered, the faecal loss is

by far the most important. Even for a food of high digestibility like barley, twice as much energy is lost in the faeces as in the urine and methane. The main factors affecting the metabolisable energy values of a food are therefore those which influence its digestibility. These have been discussed earlier (Chapter 10), and the emphasis here will be on urine and methane losses.

TABLE 11.2 Metabolisable Energy Values of some typical Foods (Not corrected for Plane of Nutrition or for Nitrogen Balance)
(All values are expressed in kcal per lb food dry matter)

Food	Animal	Gross energy	Energy lost in			Metabolisable energy
			Faeces	Urine	Methane	
Maize	Steer	2050	309	88	138	1515
Maize	Pig	2051	175	41	—	1835
Maize	Fowl	2010	240			1770
Wheat	Fowl	1970	310			1660
Oats (ground)	Fowl	2130	760			1370
Oats (fine ground)	Fowl	2090	670			1420
Barley	Fowl	1980	530			1450
Barley meal	Pig	1898	301	61	—	1536
Barley meal	Cow	1989	449	86	123	1331
Oats (ground)	Pig	2103	599	67	—	1437
Wheat bran	Steer	2060	653	109	154	1144
Coconut cake meal	Pig	2061	692	284	—	1085
Dried ryegrass (young)	Sheep	2112	370	165	177	1400
Dried ryegrass (mature)	Sheep	2060	770	70	150	1070
Meadow fescue hay (young)	Sheep	1955	583	97	163	1112
Meadow fescue hay (mature)	Sheep	1947	822	61	148	916
Lucerne hay	Steer	1990	888	104	140	858

The metabolisable energy value of a food will obviously vary according to the species of animal to which it is given. In non ruminants energy losses as methane are negligible, which means that for foods such as concentrates which are digested to much the same extent by ruminants and non ruminants, metabolisable energy values will be greater for the non ruminants. This is illustrated in Table 11.2, where values for barley given to cattle, pigs and fowls are compared. Differences between cattle and sheep in urine and methane losses of energy are, like those in faecal losses, small and of no significance.

The metabolisable energy value of a food will vary according to whether the amino acids it supplies are retained by the animal for

protein synthesis, or are deaminated and their nitrogen excreted in the urine as urea. In the latter case the energy excreted in the urine will be greater by 2.53 kcal/g urea excreted (or 5.4 kcal/g urinary nitrogen). For this reason metabolisable energy values are frequently corrected to zero nitrogen balance. The factor used in the correction is greater than 5.4 kcal/g urinary nitrogen, because some nitrogen is excreted in compounds containing more energy per g nitrogen than urea contains. For ruminants a factor of 7.45 kcal/g nitrogen has been used, and for poultry one of 8.22 (poultry excrete much nitrogen as uric acid, which has a calorific value of 2.74 kcal/g or 8.22 kcal/g nitrogen). If an animal is excreting more nitrogen in its urine than it is absorbing from its food (i.e. is in negative nitrogen balance—see Chapter 13), some of the urine nitrogen is not derived from the food, and in this case the metabolisable energy value must be subjected to a positive correction.

The manner in which the food is prepared may in some cases affect its metabolisable energy value. For ruminants the grinding and pelleting of roughages leads to an increase in faecal losses of energy, but this may be partly offset by a reduction in methane production. For poultry the grinding of cereals has no consistent effect on metabolisable energy values.

A factor of considerable importance in determining the metabolisable energy value of foods for ruminants is the quantity given or *level of feeding*. This is best defined in relation to the energy requirement of the animal, an intake of food supplying energy just sufficient for maintenance being regarded as having unit value. In fully fed non-lactating animals the level of feeding may increase to a maximum of about three times the maintenance level. The effect of doubling the level of feeding, from maintenance to twice maintenance, is to increase faecal losses of energy by up to 10 kcal per 100 kcal food energy, to reduce losses of methane by about 1 kcal per 100 kcal and to reduce urine losses to a smaller extent. The additional losses in faeces caused by increasing intake are less for highly digestible foods than for materials of poorer quality. The overall effect of doubling intake is to depress the metabolisable energy value at the maintenance level by less than 5 per cent. for foods high in metabolisable energy, but by as much as 15 per cent. for poor-quality foods.

The Heat Increment of Foods

The ingestion of food by an animal is followed by losses of energy not only as the chemical energy of its solid, liquid and gaseous excreta but also as heat. Animals are continuously producing heat and losing it to

their surroundings, either directly by radiation, conduction and convection, or indirectly by the evaporation of water. If a fasting animal is given food, within a few hours its heat production will increase above the level represented by basal metabolism. This increase is known as the heat increment or specific dynamic effect of the food, it is quite marked in Man after a large meal. The heat increment may be expressed in absolute terms (kcal/g food dry matter), or relatively as a proportion of the gross or metabolisable energy. Unless the animal is in a particularly cold environment, this heat energy is of no value to it, and must be considered, like the energy of the excreta, as a tax on the energy of the food.

The main cause of the heat increment is the energetic inefficiency of the reactions by which absorbed nutrients are metabolised. For example, it was shown in Chapter 9 that if glucose is oxidised in the formation of ATP, the efficiency of free energy capture is only about 68 per cent, 32 per cent being lost as heat. The same inefficiency is apparent in syntheses of body constituents. The linking of one amino acid to another, for example, requires the expenditure of six pyrophosphate 'high energy' bonds, and if the ATP which provides these is obtained through glucose oxidation, about 100 kcal of energy will be lost as heat for each peptide linkage formed (i.e. about 800 kcal/kg protein formed).

A further part of the heat increment is attributable to the processes of digestion. Energy is used for the mastication of food and for its propulsion through the alimentary tract, and since chemical energy used for work performed within the body is converted into heat there will be a consequent increase in the animal's heat production. In ruminant animals particularly, some heat arises from the activity of the micro organisms of the alimentary tract, this is known as the *heat of fermentation*. It is estimated to amount to about 5-10 per cent of the gross energy of the food.

Net Energy and Energy Retention

The deduction of the heat increment of a food from its metabolisable energy gives the *net energy* value of the food. The net energy of a food is that energy which is available to the animal for useful purposes, i.e. for body maintenance and for the various forms of production.

Net energy used for maintenance is mainly used to perform work within the body, and will leave the animal as heat. That used for growth and fattening and for milk, egg or wool production is either

stored in the body or leaves it as chemical energy, and the quantity so used is referred to as the animal's *energy retention*.

The fate of the gross energy of foods is summarised in Fig. 11.1. It is important to understand that of the heat lost by the animal only a part, the heat increment of the food, is truly waste energy which can be regarded as a direct tax on the food energy. The heat resulting from the energy used for body maintenance is considered to represent energy which has been used by the animal and degraded into a useless form during the process of utilisation.

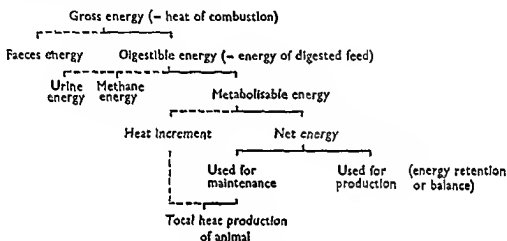


FIG. 11.1. The partition of food energy in the animal.

ANIMAL CALORIMETRY: METHODS FOR MEASURING HEAT PRODUCTION AND ENERGY RETENTION

In order to study the extent to which the metabolisable energy of the food is utilised by the animal, it is necessary to measure either the animal's heat production or else its energy retention. Examination of Fig. 11.1 will make it clear that, if one of these quantities is known, the other can be determined by subtracting the known one from the metabolisable energy. Heat production can be measured directly by physical methods; an animal calorimeter is required and the process is known as *direct calorimetry*. Alternatively, heat production can be estimated from the respiratory exchange of the animal; for this a respiration chamber is normally used and the approach is one of *indirect calorimetry*. Respiration chambers can also be used to estimate energy retention rather than heat production, by the procedure known as the *carbon and nitrogen balance trial*.

Direct Calorimetry

Animals do not store heat, except for relatively short periods of time, and when measurements are made over periods of 24 hours or longer it is generally safe to assume that the quantity of heat lost from the animal is equal to the quantity produced. Heat is lost from the body principally by radiation, conduction and convection from the body surface and by evaporation of water from the skin and lungs. The

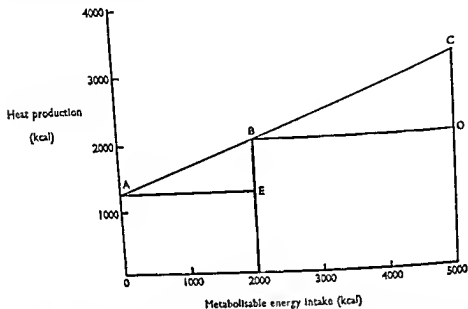


FIG 11.2 The difference method for estimating the heat increment of foods. A is the basal metabolism and B and C represent heat production at metabolisable energy intakes of 2000 and 5000 kcal respectively. For the sake of simplicity the relation between heat production and metabolisable energy intake is shown here as being linear, i.e. ABC is a straight line, however, as explained later in the chapter, this is not usually the case.

animal calorimeter is basically an airtight and insulated chamber. Evaporative losses of heat are measured by recording the volume of air drawn through the chamber and its moisture content on entry and exit. In most early calorimeters the sensible heat loss (i.e. that lost by radiation, conduction and convection) was taken up in water circulated through coils within the chamber, the quantity of heat removed from the chamber could then be computed from the rate of flow of the water and the difference between its entry and exit temperatures. In a more recent type, the *gradient layer calorimeter*, the quantity of heat is measured electrically as it passes through the wall of the chamber.

This type of calorimeter lends itself well to automation, and both sensible and evaporative losses of heat can be recorded automatically. Most calorimeters incorporate apparatus for measuring respiratory exchange and can therefore be used for indirect calorimetry as well.

The heat increment of the food under investigation is determined as the difference in the heat production of the animal at two levels of intake, as shown in Fig. 11.2. Two levels are needed because a part of the animal's heat production is contributed by its basal metabolism. An increase in food intake causes total heat production to rise, but the basal metabolism is assumed to remain the same. The increase in heat production can thus be attributed to the heat increment of the extra food given.

In the example shown in Fig. 11.2, the food was given at levels supplying 2000 and 5000 kcal metabolisable energy. The increment of 3000 kcal (*BD* on the figure) was associated with an increase in heat production, *CD*, of 1200 kcal. The heat increment as a percentage was therefore:

$$100 \text{ } CD/BD \text{ or } 100 \times 1200/3000 = 40 \text{ per cent.}$$

It is also possible to make the lower level of intake zero, and to estimate the heat increment as the difference in heat production between the basal (or fasting) metabolism and that produced in the fed animal. In the example of Fig. 11.2 this method gives the heat increment as $100 \text{ } BE/AE$ or $100 \times 800/2000 = 40 \text{ per cent.}$, as before.

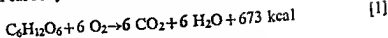
If a single food is being investigated, it may be given as the sole item of diet at both levels. If the food is one which would not normally be given alone, the lower level may be obtained by giving a basal ration and the higher level by the same basal ration *plus* some of the food under investigation. For example, the heat increment of barley eaten by sheep could be measured by feeding the sheep first on a basal ration of hay and then on an equal amount of the same hay *plus* some of the barley.

Animal calorimeters are expensive to build and the earlier types required much labour to operate them. Because of this most animal calorimetry today is carried out by the indirect method described below.

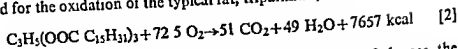
Indirect Calorimetry by the Measurement of Respiratory Exchange

The substances which are oxidised in the body, and whose energy is therefore converted into heat, fall mainly into the three nutrient classes of carbohydrates, fats and proteins. The overall reaction for the

oxidation of a carbobydrate such as glucose is



and for the oxidation of the typical fat, tripalmitin, is



In an animal obtaining all its energy by the oxidation of glucose, the utilisation of 1 litre of oxygen would lead to production of $673/(6 \times 22.4) = 5.007$ kcal of heat, for mixtures of carbohydrates an average value is 5.047 kcal per litre. Such values are known as *thermal equivalents* of oxygen, and are used in indirect calorimetry to estimate heat production from oxygen consumption. For an animal katabolising mixtures of fats alone, the thermal equivalent of oxygen is 4.686 kcal per litre (cf 4.715 kcal per litre calculated from equation [2] above).

Animals do not normally obtain energy exclusively from either carbohydrate or fat. They oxidise a mixture of these (and of protein also), so that in order to apply the appropriate thermal equivalent when converting oxygen consumption to heat production it is necessary to know how much of the oxygen is used for each nutrient. The proportions are calculated from what is known as the *respiratory quotient* (RQ). This is the ratio between the volume of carbon dioxide produced by the animal and the volume of oxygen used. Since, under the same conditions of temperature and pressure, equal volumes of gases contain equal numbers of molecules, the RQ can be calculated from the molecules of carbon dioxide produced and oxygen used. From equation [1] the RQ for carbohydrate is calculated as $6 \text{CO}_2/6 \text{O}_2 = 1$ and from equation [2] that of the fat, tripalmitin, as $51 \text{CO}_2/72.5 \text{O}_2 = 0.70$. If the RQ of an animal is known, the proportions of fat and carbohydrate oxidised can then be determined from standard tables. For example an RQ of 0.9 indicates the oxidation of a mixture of 67.5 per cent carbohydrate and 32.5 per cent fat, and the thermal equivalent of oxygen for such a mixture is 4.924 kcal per litre.

The mixture oxidised generally includes protein. The quantity of protein katabolised can be estimated from the output of nitrogen in the urine, 0.16 g of urinary N being excreted for each gram of protein. The heat of combustion of protein (i.e. the heat produced when it is completely oxidised) varies according to the amino acid proportions but averages 5.3 kcal per g. Protein, however, is incompletely oxidised in animals because the body cannot oxidise nitrogen, and the average amount of heat produced by the katabolism of 1 g of protein is 4.3

kcal. For each gram of protein oxidised, 0.77 litres of carbon dioxide are produced and 0.96 litres of oxygen used, giving an RQ of 0.8.

Heat is produced not only when organic nutrients are oxidised but also when they are used for the synthesis of tissue materials. It has been found, however, that the quantities of heat produced during these syntheses bear the same relation to the respiratory exchange as they do when the nutrients are completely oxidised.

The relation between respiratory exchange and heat production is disturbed if the oxidation of carbohydrate and fat is incomplete. This situation arises in the metabolic disorder known as ketosis, when fatty acids are not completely oxidised to carbon dioxide and water, and carbon and hydrogen leave the body as ketones or ketone-like substances. Incomplete oxidation occurs also under normal conditions in ruminants, where an end-product of carbohydrate fermentation in the rumen is methane. In practice heat production calculated from respiratory exchange in ruminants is corrected for this effect by the deduction of 0.5 kcal for each litre of methane. An alternative means of overcoming difficulties of this kind is to calculate heat production from oxygen consumption alone. If a respiratory quotient of 0.82 and a thermal equivalent of 4.8 are assumed, departures from this RQ of between 0.7 and 1.0 cause a maximum bias of no more than 3.5 per cent. in the estimate of heat production. A further simplification is possible in respect of protein metabolism. The thermal equivalent of oxygen used for protein oxidation is 4.5 kcal per litre, not very different from the value of 4.8 assumed for carbohydrate and fat oxidation. If only a small proportion of the heat production is caused by protein oxidation it is unnecessary to assess it separately, and so urinary nitrogen output need not be measured.

An example of the calculation of heat production from respiratory exchange is shown in Table 11.3.

Apparatus for Measuring Respiratory Exchange

The apparatus most commonly used for farm animals is a respiration chamber, which may be of either the *open circuit* or *closed circuit* type. In both types the central feature is an airtight container for the animal which incorporates devices allowing the feeding and watering (and even milking) of the animal, and the collection of its faeces and urine, without the chamber air mixing with the atmosphere. In the open circuit type (Fig. 11.3a), air is drawn through the chamber and then discharged. During its passage it increases in carbon dioxide content and decreases in oxygen, and the amounts of carbon dioxide

produced and oxygen used can be calculated by comparing the volume and composition of the air entering and leaving the chamber. In the closed circuit type (Fig. 11.3*b*), air is circulated from the chamber through carbon dioxide and water absorbers and back to the chamber. Oxygen used by the animal is replaced by a metered supply of the pure gas. The weight of carbon dioxide produced is determined as the increase in weight of the absorbent (generally potassium hydroxide

TABLE 11.3. Calculation of the Heat Production of a Calf from Values for its Respiratory Exchange and Urinary Nitrogen Excretion
(After K. L. Blaxter, N. McC. Graham and J. A. F. Rook, 1955, *J. agric. Sci.*, 45, 10)

<i>Results of the experiment (per 24 hours)</i>		
Oxygen consumed		392.0 litres
Carbon dioxide produced		310.7 litres
Nitrogen excreted in urine		14.8 g
<i>Heat from protein metabolism</i>		
Protein oxidised	(14.8 × 6.25)	92.5 g
Heat produced	(92.5 × 4.3)	398 kcal
Oxygen used	(92.5 × 0.96)	88.8 litres
Carbon dioxide produced	(92.5 × 0.77)	71.2 litres
<i>Heat from carbohydrate and fat metabolism</i>		
Oxygen used	(392.0 - 88.8)	303.2 litres
Carbon dioxide produced	(310.7 - 71.2)	239.5 litres
Non-protein respiratory quotient		0.79
Thermal equivalent of oxygen when RQ = 0.79		4.79 kcal/litre
Heat produced	(303.2 × 4.79)	1452 kcal
<i>Total heat produced</i>		1850 kcal

or soda lime). Both oxygen consumption and carbon dioxide production must be corrected for any differences in the amounts present in the circuit air at the beginning and end of the experiment. Methane is allowed to accumulate in the circuit air, and the amount present is determined at the end of the experiment.

Both types have their disadvantages. The open circuit requires elaborate apparatus for measuring and sampling the air, and very accurate gas analysis. Great accuracy is needed in order to measure the rather small differences in composition between in- and outgoing air. Greater differences can be induced by slowing down the rate of passage of air, but this leads to discomfort in the animal as a result of high concentrations in its atmosphere of carbon dioxide and of water vapour. These disadvantages do not obtain with the closed circuit apparatus, where the greatest drawback is the large quantities of

absorbents needed. A cow, for example, requires about 100 kg soda lime to absorb the carbon dioxide it produces each day, and 250 kg silica gel to absorb water vapour.

Respiratory exchange can be measured without an animal chamber if the subject is fitted with a face mask, which is then connected to

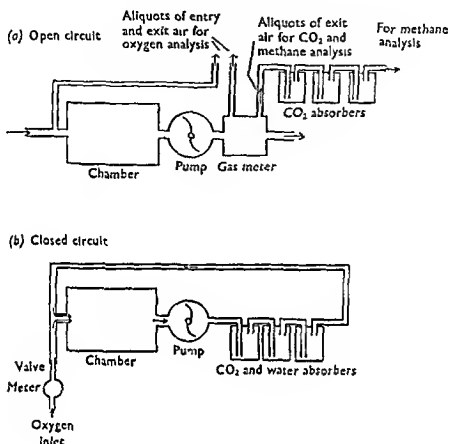


FIG. 11.3. Diagrams of respiration chambers.

either a closed or an open circuit for determining oxygen consumption alone or both oxygen consumption and carbon dioxide production. This method is suitable for short periods of measurement, but cannot be used to estimate heat production when the animal is eating.

Measurement of Energy Retention by the Carbon and Nitrogen Balance Technique

The main forms in which energy is stored by the growing and fattening animal are protein and fat, for the carbohydrate reserves of the body are small and relatively constant. The quantities of protein and fat stored can be estimated by carrying out a carbon and nitrogen balance trial; that is, by measuring the amounts of these elements

entering and leaving the body and so, by difference, the amounts retained. The energy retained can then be calculated by multiplying the quantities of nutrients stored by their calorific values.

Both carbon and nitrogen enter the body only in the food, and nitrogen leaves it only in faeces and urine. Carbon, however, leaves the body also in methane and carbon dioxide, and the balance trial must therefore be carried out in a respiration chamber. The procedure for calculating energy retention from carbon and nitrogen balance data is best illustrated by considering an animal in which storage of both fat and protein is taking place. In such an animal intakes of carbon and nitrogen will be greater than the quantities excreted, and the animal is said to be in positive balance with respect to these elements. The quantity of protein stored is calculated by multiplying the nitrogen balance by $100/16$ ($= 6.25$), for body protein is assumed to contain 16 per cent nitrogen. It also contains 51.2 per cent carbon, and the amount of carbon stored as protein can therefore be computed. The remaining carbon is stored as fat, which contains 74.6 per cent carbon. Fat storage is therefore calculated by multiplying the carbon balance, less that stored as protein, by $100/74.6$. The energy present in the protein and fat stored is then calculated by using average calorific values for body tissues. These values vary from one species to another, for cattle and sheep those used are commonly 9.37 kcal per g for fat and 5.32 kcal per g for protein. An example of this method of calculating energy retention (and heat production) is shown in Table 11.4.

Other Methods for Measuring Energy Retention

Because calorimetric experiments require elaborate apparatus and can be conducted with only small numbers of animals, numerous attempts have been, and are still being, made to measure energy retention in other ways. In many feeding trials the animals' intakes of digestible or metabolisable energy can be measured satisfactorily but their energy retention can be estimated only from changes in liveweight. Weight changes, however, provide most inaccurate estimates of energy retention, firstly because they may represent no more than changes in the contents of the gut or bladder, and secondly because the energy content of true tissue gain can vary over a wide range according to its proportions of bone, muscle and fat (see Chapter 14). These objections are only partly overcome in experiments where the energy retention is in the form of milk or eggs, whose energy is easily measured, for retention in these products is almost invariably accompanied by

retention in other tissues (e.g. milking cows are normally increasing or decreasing in liveweight and in energy content).

Energy retention can, however, be measured in feeding trials if the energy content of the animal is estimated at the beginning and end of the experiment. In the *comparative slaughter method* this is done by dividing the animals into two groups and slaughtering one (the sample slaughter group) at the beginning of trial. The energy content of the

TABLE 11.4. Calculation of the Energy Retention and Heat Production of a Sheep from its Carbon and Nitrogen Balance
(After K. L. Blaxter and N. McC. Graham, 1955, *J. agric. Sci.*, 46, 292)

Results of the experiment (per 24 hours)

	C (g)	N (g)	Energy (kcal)
Intake	684.5	41.67	6791
Excretion in faeces	279.3	13.96	2741
Excretion in urine	33.6	25.41	359
Excretion as methane	20.3	—	356
Excretion as CO ₂	278.0	—	—
Balance	73.3	2.30	—
Intake of metabolisable energy	—	—	3335

Protein and fat storage

Protein stored	(2.30×6.25)	14.4 g
Carbon stored as protein	(14.4×0.512)	7.4 g
Carbon stored as fat	$(73.3 - 7.4)$	65.9 g
Fat stored	$\left(65.9 \times \frac{100}{74.6}\right)$	88.3 g

Energy retention and heat production

Energy stored as protein	(14.4×5.32)	77 kcal
Energy stored as fat	(88.3×9.37)	827 kcal
Total energy retention	$(77 + 827)$	904 kcal
Heat production	$(3335 - 904)$	2431 kcal

animals slaughtered is determined by bomb calorimetry, the samples used being taken either from the whole, muned body or from the tissues of the body after these have been separated by dissection. A relationship is then obtained between the liveweight of the animals and their energy content, and this is used to predict the initial energy content of animals in the second group. The latter are slaughtered at the end of the trial and treated in the same manner as those in the sample slaughter group, and their energy gains can then be calculated.

The comparative slaughter method requires no elaborate apparatus, but is obviously expensive and laborious when applied to larger animal

Table 11.5 shows also that dietary fat is used for maintenance with high energetic efficiency, as one would expect. When protein is used to provide energy for maintenance, however, there is an appreciable heat increment of about 20 per cent, which is in part attributable to the energy required for urea synthesis (see Chapter 9). In ruminants, energy for maintenance is absorbed largely in the form of volatile fatty acids. Experiments in which the pure acids have been infused singly into the rumens of fasting sheep have shown that there are differences between them in the efficiency with which their energy is utilised (Table 11.5). But when the acids are combined into mixtures representing the extremes likely to be found in the rumen, the efficiency of utilisation is uniform and high. Nevertheless the efficiency is still less than that for glucose, and this discrepancy, together with the energy lost through heat of fermentation in ruminants, leads one to expect that metabolisable energy will be utilised more efficiently for maintenance in those animals in which it is absorbed in the form of glucose than in ruminants.

Very few experiments have been carried out to determine the efficiency with which the metabolisable energy in foods is used for maintenance, and these few have been restricted almost entirely to ruminant animals fed on roughages. A selection of the results is given in Table 11.5. Most of the metabolisable energy of the foods shown would have been absorbed in the form of volatile fatty acids. Efficiency of utilisation is less, however, than for synthetic mixtures of these acids, since with whole foods heat losses are increased by heat of fermentation and by the energy used for work of digestion. In spite of this, the metabolisable energy in these foods was used with quite high efficiency.

Utilisation of Metabolisable Energy for Productive Purposes

Although energy may be stored by animals in a wide variety of products—in body fat, muscle, milk, eggs and wool—the energy of these products is contained mainly in fat and protein (only in milk is much energy stored as carbohydrate). The efficiency with which metabolisable energy is used for productive purposes therefore depends largely on the energetic efficiency of the metabolic pathways involved in the synthesis of fat and protein from absorbed nutrients. These pathways have been outlined in Chapter 9. In general the synthesis of either fat or protein is a more complicated process than its catabolism, in the same way that the construction of a building is more difficult than its demolition. Not only must the building materials be present in the right proportions, but they must arrive on the scene at the right time, and the absence of a particular material may prevent or seriously impair

the whole process. Thus it was shown in Chapter 9 that fatty acid synthesis is dependent on a supply of NADPH. Because of the greater complexity of synthetic processes it is more difficult to estimate their theoretical efficiency.

From the reactions involved, the efficiency of fat synthesis from glucose, expressed as kcal fat formed per 100 kcal glucose used, can be shown to have a theoretical value of the order of 70 per cent.; a higher value would be expected for fat synthesis from absorbed glycerides. If, as in ruminants, the substrate is largely volatile fatty acids, efficiency will be lower than 70 per cent. In protein synthesis the energy cost of linking amino acids together is relatively small, and if these are present in the right proportions the theoretical efficiency of protein synthesis is about 80 per cent. If however some amino acids have to be synthesised and others undergo deamination, efficiency will be considerably less. The synthesis of lactose from glucose can be achieved with an efficiency of close to 100 per cent., but in the dairy cow the glucose so utilised will largely be formed from propionic acid, or possibly from amino acids (gluconeogenesis), and the efficiency of lactose synthesis will be reduced.

The figures given above are all calculated from the appropriate metabolic pathways, and in relating them to the efficiency with which metabolisable energy will be utilised it is important to remember that they will be reduced by those energy losses mentioned earlier (p. 162) which are directly referable to the consumption, digestion and absorption of food.

Measuring in an animal the energetic efficiency with which a single substance such as protein, or a single product such as milk, is synthesised is complicated by the fact mentioned previously that animals seldom store energy as single substances or even as single products. An exception however is the mature, non-lactating and non-pregnant animal, for which it is considered that almost all energy storage is in the form of body fat. Because of this, it is the process of fattening in mature animals which has been most extensively studied in connection with energetic efficiency. Considerably less is known about the efficiency of utilisation of metabolisable energy in growing animals (i.e. in those storing appreciable quantities of energy in protein as well as in fat), in those producing milk or eggs, or, least of all, in those where energy is stored in the foetus and associated structures.

Tables 11.6 and 11.7 give examples of the efficiency with which metabolisable energy in various nutrients and foods respectively has been found to be utilised for fattening in mature animals. In general there is

species It would be an advantage if the body composition of an animal, and hence its energy content, could be measured in the living animal, or, failing that, in the whole, undissected carcass Several attempts have been made to estimate body composition in living animals, but so far none has led to a sufficiently accurate method A promising approach depends on the relation existing between the fat content of an animal and its specific gravity or that of its carcass Fat has an appreciably lower specific gravity than bone and muscle, and the fatter an animal, the lower is its specific gravity

FACTORS AFFECTING THE UTILISATION OF METABOLISABLE ENERGY

The efficiency of utilisation of metabolisable energy in the animal is defined as that proportion of it which is retained, or

$$\frac{\text{change in energy retention}}{\text{change in metabolisable energy intake}} \times 100$$

It is therefore the complement of the heat increment when the latter is expressed as a percentage of the metabolisable energy For example, if food supplying 1000 kcal metabolisable energy were given to an animal and its energy retention increased by 600 kcal, the efficiency of utilisation would be 60 per cent (and the heat increment 40 per cent of the metabolisable energy)

The efficiency with which metabolisable energy is utilised depends on the interaction of two principal factors, these being the nature of the chemical compounds in which the metabolisable energy is contained and the purpose for which these compounds are used by the animal

Utilisation of Metabolisable Energy for Maintenance

For maintenance purposes the animal oxidises the nutrients absorbed from its food principally to provide energy for work If it is given no food, it obtains this energy mainly by the oxidation of body fat When food is given, but in quantities insufficient to provide all the energy needed for maintenance, the task of providing ATP is partially transferred from the reserves of body fat to the nutrients absorbed If the energy contained in these nutrients can be transferred to ATP as efficiently as can that in body fat, no extra heat will be produced by the animal apart from that associated specifically with the consumption, digestion and absorption of food (Heat of fermentation comes into this category, and also work of digestion, that is, heat arising from the energy used in the mastication of food and its

propulsion through the gut, in the absorption of nutrients and in their transport to the tissues)

The efficiency of free energy capture when body fats are oxidised and ATP is formed can be calculated from the reactions shown in

TABLE 11.5. Efficiency of Utilisation for Maintenance of Metabolisable Energy in various Nutrients and Foods

<i>Food or nutrient</i>	<i>Animal</i>	<i>Efficiency, per cent</i>
<i>Carbohydrates</i>		
Glucose	Dog	95
Glucose (per rumen)	Sheep	94
Glucose (per abomasum)	Sheep	100
Starch	Rat	88
<i>Fats</i>		
Olive oil	Dog	95
Olive oil	Rat	99
<i>Proteins</i>		
Casein	Rat	76
Casein (per abomasum)	Sheep	82
<i>Volatile fatty acids</i>		
Acetic	Sheep	59
Propionic	Sheep	86
Butyric	Sheep	76
Mixture A (25 C ₂ 45 C ₃ 30 C ₄)	Sheep	87
Mixture B (75 C ₂ 15 C ₃ 10 C ₄)	Sheep	86
<i>Roughages</i>		
Dried ryegrass (young)	Sheep	78
Dried ryegrass (mature)	Sheep	74
Meadow fescue hay (young)	Sheep	69
Meadow fescue hay (mature)	Sheep	74
Lucerne hay	Steer	66
Sudan grass hay	Cow	75
<i>Concentrates</i>		
Maize	Sheep	78
Maize	Steer	82

Chapter 9 to be of the order of 65 per cent. For glucose, to take an example of a nutrient, the efficiency is also about 65 per cent. One would therefore expect that glucose given to a fasting animal would be utilised without any increase in heat production, or in other words with apparent (calorimetric) efficiency of 100 per cent. Table 11.5 shows that this is approximately true. In sheep the efficiency is reduced through fermentation losses if the glucose passes into the rumen, but these losses are avoided if it is infused directly into the abomasum.

reasonable agreement between the values shown in the tables and the theoretical considerations given previously. In the case of the pure nutrients, non-ruminants utilise fat more efficiently than carbohydrate, and carbohydrate more efficiently than protein. The values for pure nutrients given to poultry, however, are surprisingly low, both when compared with those for pigs in the same table and with those for poultry foods in Table 11.7, they require further investigation. As in Table 11.5, the figures for ruminants are lower than those for non-ruminants. Individual fatty acids are used with varying efficiency for fattening, as they are for maintenance, but for fattening this variability is conveyed to the mixtures of acids. Those in which acetic acid predominates are used much less efficiently than those richer in the higher acids, and even the latter are less efficiently utilised than glucose. This, together with the heat of fermentation, explains why glucose given via the rumen, and therefore fermented, promotes less fat storage than that given via the abomasum and absorbed unchanged. The differences between ruminants and non-ruminants occur again in Table 11.7, although there is little information available for poultry.

A comparison of Tables 11.6 and 11.7 on the one hand with Table 11.5 on the other reveals two striking differences. In the first place, values for fattening are appreciably lower than those for maintenance. This is doubtless due in part to the greater complexity of anabolic processes, but also to the fact that heat increments of foods determined below maintenance represent not the true inefficiency of energy conversion,

TABLE 11.6 Efficiency of Utilisation for Fattening of Metabolisable Energy in Pure Nutrients

Nutrient	Efficiency (per cent) in			
	Cattle	Sheep	Pigs	Fowls
Starch	64	64	76	57
Groundnut oil	59	58	86	78
Proteins (various)	50	52	62	55
Glucose (per rumen)	—	54	—	—
Glucose (per abomasum)	—	72	—	—
Casein (per rumen)	—	50	—	—
Casein (per abomasum)	—	65	—	—
<i>Volatile fatty acids</i>				
Acetic	—	33	—	—
Propionic	—	56	—	—
Butyric	—	62	—	—
Mixture A (25 C ₂ 45 C ₃ 30 C ₄)	—	58	—	—
Mixture B (75 C ₂ 15 C ₃ 10 C ₄)	—	32	—	—

but inefficiency relative to that of the utilisation of body fat. This is illustrated in Figure 11.4. As metabolisable energy intake rises from zero to the maintenance level (i.e. distance AC in the figure), heat production rises by distance BC . At maintenance the apparent heat increment is therefore $100 BC/AC$, or in other words basal metabolism is the base line for the calculation. In the fasting animal a proportion of the total heat production arises during the transference of energy from body fat to ATP (distance AE). In effect, this represents the heat increment of body fat. As food intake increases to the level needed for maintenance, the heat arising from the metabolism of body fat decreases (triangle ADE) and that arising from the utilisation of food constituents increases (triangle ABD). The proportion $100 BD/AC$ therefore provides a more accurate estimate of the efficiency with which metabolisable energy is used for maintenance. The base line in this case, DE , is known as the *minimum base value of heat production*. Above maintenance the heat increment is given by the expression $100 FG/BG$.

The second important difference between efficiency values for maintenance and for fattening lies in the variability encountered in foods for ruminants. In Table 11.5 the variability is quite small, the extreme values being lucerne hay, 66, and maize, 82 (a difference of 22 per cent of the mean). In Table 11.7, however, the range for foods comparable with those of Table 11.5 is from 34 for mature ryegrass to 59 for maize

TABLE 11.7 Efficiency of Utilisation for Fattening of Metabolisable Energy in various Foods

<i>Food</i>	<i>Animal</i>	<i>Efficiency (per cent)</i>
<i>Roughages</i>		
Dried ryegrass (young)	Sheep	52
Dried ryegrass (mature)	Sheep	34
Meadow fescue hay (young)	Sheep	41
Meadow fescue hay (mature)	Sheep	35
Wheat straw	Steer	24
<i>Concentrates</i>		
Barley meal	Steer	59
Barley meal	Pig	87
Maize meal	Sheep	59
Maize meal	Pig	74
Maize meal	Fowl	82
Ground oats	Pig	83
Ground oats	Fowl	83
Groundnut meal	Steer	56
Groundnut meal	Pig	71
Coconut cake meal	Steer	50
Coconut cake meal	Pig	72

and barley, a difference of 53 per cent of the mean. It appears that, while foods generally are used less efficiently for fattening than for maintenance, the ratio between the two efficiency values is not the same for all foods. Thus in maize metabolisable energy is used $100 \times 59/78$ or 76 per cent as efficiently for fattening as for maintenance, whereas the comparable value for mature fescue hay is $100 \times 35/74$, 47 per cent. In general, as the metabolisable energy content of foods declines, the

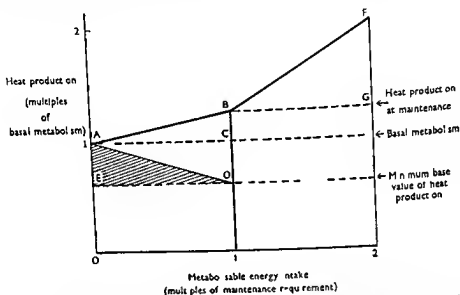


FIG. 11.4 Relationship between heat production and metabolisable energy intake. Total heat production is represented by line ABF. Other points are explained in the text.

efficiency of utilisation of the metabolisable energy also declines, but this fall in efficiency is relatively greater when energy is used for production than when it is used for maintenance. The explanation for this is believed to be that foods of low digestibility, and therefore of low metabolisable energy, are high in fibre and give rise to volatile fatty acid mixtures rich in acetic acid, a high proportion of acetic acid has only a small influence on utilisation for maintenance but a much greater effect on that for fattening. In addition it is possible that with concentrated foods more carbohydrate escapes fermentation and is absorbed as glucose.

Utilisation of metabolisable energy for growth In immature, growing animals a considerable proportion of the energy stored is retained in the form of protein. Since protein synthesis has a theoretical maximal efficiency which is greater than that for fat synthesis, it is likely that

metabolisable energy can be used more efficiently in growing than in fattening animals. There have been few studies of energy utilisation in immature animals, but there is evidence that in both cattle and sheep metabolisable energy is utilised up to 30 per cent. more efficiently for growth than for fattening.

Utilisation of metabolisable energy for milk production. For milk synthesis also theoretical considerations point to a more efficient utilisation of metabolisable energy than for fattening, since in cow's milk about half the energy is contained in protein and carbohydrate. In addition, the fatty acids of milk fat have an average molecular weight lower than that of body fat and should therefore be synthesised with greater energetic efficiency. In experiments in which cows were kept on a constant food intake but in which milk secretion was partially suppressed by incomplete milking, the nutrients spared from milk synthesis were diverted to body fat synthesis, and it was found that, for each reduction of 100 kcal of milk, 83 kcal were stored as body fat. This suggests that milk secretion is about 20 per cent. more efficient than fattening.

The average efficiency of conversion of metabolisable energy to milk is considered to be about 70 per cent., which is greater than the values for fattening shown in Table 11.7 and approaches the values for maintenance of Table 11.5. Milk secretion is also intermediate between maintenance and fattening in respect of the effect on efficiency of the relative proportions of the fatty acids found in the rumen. Over the range of diets and of acid mixtures normally experienced by cows, the effect of the acid proportions is thought to be smaller than on efficiency of utilisation for fattening. It is known, however, that unusually low proportions of acetic acid and high proportions of propionic will depress milk fat synthesis (see Chapter 15).

Other Factors affecting the Utilisation of Metabolisable Energy

Associative effects. In Chapter 10 it was explained that the digestibility of a food can vary according to the nature of the ration in which it is included. Associative effects of this kind have also been observed in the utilisation of metabolisable energy. In one experiment it was found that the metabolisable energy of maize meal was utilised with an apparent efficiency for fattening varying between 58 and 74 per cent. according to the nature of the basal ration to which it was added. In ruminants, such differences are likely to arise through variations in the effect of the food on the manner in which the whole ration is digested, and hence on the form in which metabolisable energy is

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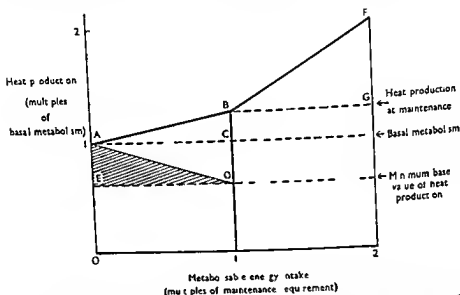


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absorbed. The implication is that values for the efficiency of utilisation of metabolisable energy for individual foods are of limited significance.

Level of feeding Increasing the quantity of food given to an animal causes both the digestible and metabolisable energy values of the food to fall. Until recently it was considered that the fall in digestibility was accompanied by a fall in the efficiency with which metabolisable energy is utilised. In other words it appeared that, as metabolisable energy intake increased, the animal used progressively less for valuable purposes and wasted progressively more as heat. If one considers overall efficiency, i.e. for maintenance and production together, then there is a decline as food intake increases from zero to the limit of appetite, but this is caused by a progressive change in the proportions of the metabolisable energy used for the relatively efficient process of maintenance and for the less efficient processes of production. For example, if the metabolisable energy of a food were used with 80 per cent efficiency for maintenance and 50 per cent for production, average efficiency at an intake providing for maintenance and at intakes two and three times as great would be 80, 65 and 60 per cent respectively. Recent experiments have shown that, at intakes between maintenance and maximum appetite, metabolisable energy is used for fattening with constant efficiency.

Balance of nutrients The effect of the nutrient proportions of the food has been partly covered in earlier parts of this section. A fattening animal will tend to use metabolisable energy more efficiently if it is provided as carbohydrate than if it is provided as protein. Similarly if a growing animal is provided with insufficient protein or with insufficient of a particular amino acid, it will tend to store energy as fat rather than as protein, and the efficiency with which it utilises metabolisable energy will probably be altered.

Deficiencies of minerals and vitamins, too, can interfere with energy utilisation. Thus a deficiency of phosphorus has been shown to reduce efficiency of utilisation by about 10 per cent in cattle. This effect is hardly surprising in view of the vital role of phosphorus in the energy-yielding reactions of intermediary metabolism.

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THE EVALUATION OF FOODS

(C) SYSTEMS FOR EXPRESSING THE ENERGY VALUE OF FOODS

For the farmer the essential steps in the scientific rationing of animals are, firstly, the assessment of their nutrient requirements, and secondly, the selection of foods which can supply these requirements. This balancing of demand and supply is made separately for each nutrient, and in many cases the nutrients given first consideration are those supplying energy. There are good reasons why energy should receive priority. In the first place the energy-supplying nutrients are those present in the food in greatest quantity; this means that if a diet has been devised to meet other nutrient requirements first and is then found to be deficient in energy, a major revision of its constituents will probably be needed. In contrast, a deficiency of a mineral or vitamin can often be rectified very simply by adding a small quantity of a concentrated source.

A further feature of the energy-containing nutrients which distinguishes them from others is the manner in which the performance of an animal, when measured as liveweight gain or milk or egg production, responds to changes in the quantities supplied. While an animal with a given level of performance, a steer gaining 1 lb per day, for example, will respond eventually if the allowance of any one nutrient is *reduced* below the quantity required for this level of performance, *increases* in single nutrients above the requirement generally have little effect. Increasing the quantity of vitamin A supplied, for example, to twice the requirement is unlikely to affect the steer's liveweight gain (although it may increase its vitamin A reserves). But if energy intake alone is increased the animal will attempt to retain more energy, either partly as protein if nitrogen intake is adequate, or entirely as fat, and its liveweight gain will increase. In effect, energy intake is the *pace-maker* of production, as animals tend to show a continuous response to changes in the quantities supplied.

If other nutrients are present in amounts only just sufficient for the animal's requirements, the response to an increase in energy intake is likely to be an undesirable one. Increasing the storage of body fat

is likely to increase the need for minerals and vitamins associated with the enzyme systems involved in fat synthesis, and so to precipitate a deficiency of those substances. It is therefore important to maintain a correct balance between energy, the pacemaker, and other nutrients in the ration.

Classification of Energy Systems

The energy value of a food can be expressed in a variety of ways, ranging from the most easily determined measure, gross energy, to the net energy value. In practice gross energy is not used in evaluating foods, and the various systems can be divided into two classes according to whether the criterion used is on the one hand digestible or metabolisable energy, or on the other hand net energy. Net energy systems appear to have the advantage in the rationing of animals, because they allow animal requirements and food values to be expressed in the same units. Thus if an animal were making liveweight gains containing 2000 kcal per lb, and a food contained 500 kcal per lb of net energy when used for body fat synthesis, the quantity of that food required to promote 1 lb of gain could be calculated quite simply as $2000/500 = 4$ lb. But if food values are expressed in terms of metabolisable energy, the calculation becomes complicated by the necessity of estimating the efficiency with which metabolisable energy is likely to be retained by the animal. This apparent superiority of net energy led the earlier investigators of energy metabolism in farm animals to devise net energy systems for evaluating foods. Later it began to be realised that, although the metabolisable energy value of a food is reasonably constant for a particular species of animal, the efficiency with which that metabolisable energy is utilised varies according to the purpose for which it is required by the animal, so that net energy values vary accordingly. This has led to modifications in net energy systems, and in some cases to their rejection. The present position is that systems based on digestible or metabolisable energy are used almost universally for pigs and poultry, and also for ruminants in the Western Hemisphere and the U.S.S.R., while net energy systems are preferred for ruminants in Europe (including the United Kingdom).

A difficulty which applies in some measure to all systems, but particularly to those based on net energy, is that the evaluation of a food is a laborious and complicated procedure. It is a procedure which cannot be applied, for example, to samples of hay or silage brought by a farmer to his advisory chemist. For this reason an essential feature of most systems is a method for predicting energy value from some

more easily measured characteristic of the food, such as its gross or digestible composition.

SYSTEMS FOR RUMINANTS

Armshy's Net Energy Values

At the beginning of this century, H. P. Armshy carried out experiments at the University of Pennsylvania in which various foods were given to steers kept in a calorimeter. These were 'difference experiments', in which the net energy value of the food was determined as the increase in energy retention resulting from an increase in food intake. The higher level of intake was generally close to the maintenance level, and so the net energy values obtained were those applying when the food was used for maintenance purposes. Because of the laborious nature of his investigations Armshy was able to evaluate only 20 foods, but he and others used the information obtained, together with the carbon and nitrogen balance data of Kellner (p. 185), in devising a method for predicting values for other foods from their content of digestible organic matter. *Estimated net energy* values, which are based on the work of Armshy and others, are now published in the standard work on the feeding of livestock under U.S.A. conditions, Morrison's *Feeds and Feeding*. They are given in the form of therms per 100 lb of food.

Armshy died in 1921, but investigations with the Pennsylvania calorimeter were continued for 20 years by others, notably E. B. Forhes. Forhes showed that the efficiency of utilisation of metabolisable energy, and therefore the net energy value of a food, varied according to whether it was used for maintenance, liveweight gain or milk production. On the other hand he considered that efficiency of utilisation of metabolisable energy for any one of these was much the same for different foods, and he quoted average efficiency values of 75, 58 and 69 per cent. for maintenance, gain and milk production. From these results it appeared that metabolisable energy would provide a satisfactory basis for evaluating foods. Net energy values have therefore been very little used in the U.S.A., where the preferred system of evaluating food energy has been the *Total Digestible Nutrients* system. This has been referred to earlier in Chapter 10, and will be discussed in more detail later in the present chapter.

Kellner's Starch Equivalents

In the last decade of the nineteenth century, O. Kellner continued a series of experiments begun by his predecessor G. Kuhn at the Möckern

Experiment Station in Germany Like Armsby he carried out difference experiments with steers, but unlike Armsby he measured energy retention by the carbon and nitrogen balance technique A more important difference between Kellner's and Armsby's experiments was that, whereas the latter used the maintenance level of nutrition as his *higher* level of intake, Kellner used this as his *lower* level Kellner's net energy values are therefore values for body fat production

A further difference between Kellner's and Armsby's work is to be found in the units they used Kellner used kilocalories in his experiments, but when reporting them he frequently expressed energy retention in terms of matter, using as his unit the weight of fat stored rather than the amount of energy retained If an animal stored protein, this was expressed as its isodynamic weight of fat, i.e. as the weight of fat containing the same quantity of energy as the protein retained Furthermore, rather than express the values of foods in absolute terms as the weight of fat stored per unit of food consumed, Kellner chose a relative measure, the fat-producing power of the food relative to the fat-producing power of that common constituent of foods, starch

In experiments in which pure starch was added to the basal, maintenance ration of a steer, Kellner found that for each 1 g digested the animal stored 0.248 g of fat When barley, to take an example of a food, was given under the same conditions, 0.20 g of fat was stored per g of dry matter consumed One gram of barley dry matter was therefore equivalent, in fat producing power, to $0.20/0.248 = 0.81$ g of starch, and this value, when multiplied by 100, is known as the *starch equivalent* of barley The starch equivalent of a food is therefore given by the expression

$$\frac{\text{weight of fat stored per unit weight of food}}{\text{weight of fat stored per unit weight of starch}} \times 100$$

It is, in other words, the net energy value of a food for fattening, relative to the net energy value of starch The calculation given above can be expressed on a net energy basis by assuming 1 g fat to contain 9.5 kcal The net energy value of starch is therefore $0.25 \times 9.5 = 2.36$ kcal per g, or 1071 kcal per lb Similarly the net energy value of barley dry matter would be $0.81 \times 1071 = 868$ kcal per lb (For the sake of simplicity, Kellner's results in the pages which follow have been converted from weights of fat to kilocalories of energy)

Kellner chose to express net energy values in terms of starch equivalents because he thought that farmers would be less familiar with calories as units of energy This argument seems illogical today when

the food calorie is a widely used term. Nevertheless starch equivalents have been adopted in many European countries and in parts of the British Commonwealth. In the U.K. the starch equivalents of foods are published in the Ministry of Agriculture bulletin *Rations for Livestock*.

Kellner and his successor, Fingerling, determined the starch equivalents of about 30 foods for cattle. Kellner also devised a method for calculating the starch equivalent of a food from the results of a digestibility trial. He began by measuring the net energy values of semi-purified substances typical of the proximate constituents of foods.

TABLE 12.1. The Net Energy Values and Starch Equivalents of Pure Nutrients as found by Kellner with Fattening Cattle

<i>Nutrient</i>	<i>Fraction of food represented</i>	<i>Net energy value of digestible nutrient (kcal/lb)</i>	<i>Net energy value relative to starch (starch equivalent)</i>
Starch	Nitrogen-free extractives	1071	1
Cellulose	Crude fibre	1091	1
Wheat gluten	Protein	1014	0.94
Groundnut oil	Ether extract of oilseeds	2582	2.41
—	Ether extract of starchby concentrates	—	2.12*
—	Ether extract of roughages	—	1.91*

* Values suggested by Kellner.

Starch was used to represent nitrogen-free extractives, straw pulp (containing 76.8 per cent. fibre) for crude fibre, wheat gluten for protein and groundnut oil for ether extract. From the results obtained, the net energy values of the proximate constituents were calculated to be as shown in Table 12.1. Although the ether extract of oilseeds was found to have a value of 2582 kcal per lb, Kellner considered that the values for ether extract in cereals and roughages would be lower because this fraction would consist to a greater extent of such non-glyceride materials as waxes and pigments.

The values shown in the last column of Table 12.1, the starch equivalents of digestible nutrients, were then used in calculating the starch equivalents of foods. Table 12.2 illustrates the calculation as applied to barley meal. The starch equivalent of barley meal when determined directly, in a full calorimetric investigation, was found to be 82, and thus not greatly different from the predicted value. In general Kellner found that for concentrated foods the actual and predicted starch

equivalents were in reasonable agreement, although there was a tendency for the predicted values to be the higher. For roughages, however, the indirect method predicted starch equivalents much higher than those found by actual measurement. For example, the meadow hay of

TABLE 12.2 Calculation of the Starch Equivalent of Barley Meal from its Digestible Nutrients

	<i>Digestible nutrient in food dry matter (per cent)</i>	<i>Starch equivalent factor</i>	<i>Starch equivalent</i>
Nitrogen free extractives	65.8	1	65.8
Crude fibre	0.2	1	0.2
True protein	11.3	0.94	10.6
Ether extract	1.6	2.12	3.4
Total			80.0

Table 12.3 was predicted to have a starch equivalent of 52.0, but the value determined by calorimetry was 32.7, a discrepancy of 37 per cent. For wheat straw the discrepancy was over 100 per cent.

Kellner attributed these discrepancies to 'work of digestion', that is, to the energy required for the mastication of food and its

TABLE 12.3 Calculation of the Starch Equivalent * of a Sample of Meadow Hay from its Digestible Nutrients

	<i>Digestible nutrient in food dry matter (per cent)</i>	<i>Starch equivalent factor</i>	<i>Starch equivalent</i>
Nitrogen free extractives	28.6	1	28.6
Crude fibre	18.0	1	18.0
True protein	3.3	0.94	3.1
Ether extract	1.2	1.91	2.3
Total			52.0*

* Uncorrected value (see p. 187 for correction)

propulsion through the digestive tract (see p. 162). The purified nutrients used in deriving the starch equivalent factors had been given to the animals in a readily assimilable form, and Kellner considered that if nutrients were contained in foods the animals would need to do work to abstract them. This work would increase heat production and thus reduce the efficiency of utilisation of metabolisable energy. He also considered that the work of digestion would be greater for foods of

low digestibility such as roughages than for highly digestible concentrates, whence the greater discrepancy between predicted and actual starch equivalents for roughages. In respect of roughages, Kellner's theory was supported by his demonstrating a close relationship between their crude fibre content and the magnitude of their starch equivalent discrepancy. He calculated that, for each 1 per cent. of crude fibre in a roughage, its true starch equivalent would be reduced by 0.58 units below the predicted value, and proposed that this factor of 0.58 should be incorporated in the prediction of the starch equivalents of dry roughages, in the following manner:

<i>Meadow hay (containing 33 per cent. crude fibre)</i>	
Starch equivalent as calculated in Table 12.3	52.0
Less 33×0.58	19.1
	<hr/>
Corrected starch equivalent	32.9

For types of roughage other than long hay and straw Kellner proposed the crude-fibre correction factors shown in Table 12.4.

No crude-fibre correction is used when predicting the starch equivalents of concentrates. Instead, Kellner allowed for the much smaller discrepancies associated with these foods by introducing a system of 'value numbers'. The value number for barley was 100, indicating that the actual starch equivalent was equal to (or 100 per cent. of) the predicted value. Other concentrates had value numbers rather less than 100; that for groundnut meal was 98, indicating that the predicted value had to be multiplied by 98/100 to give the true starch equivalent. For low-fibre concentrates the value numbers were in the range 90-100, but for more fibrous materials, such as wheat bran, they were as low as 77. At first sight this form of correction appears unsound, since the starch equivalent of a food can be predicted only through the use of a value number which would need to be obtained in a calorimetric trial. Value numbers are useful, however, in predicting the starch equivalents of foods of the same kinds as those examined by Kellner but differing slightly in composition.

Kellner was certainly correct in relating anomalies in the prediction of starch equivalents to the crude fibre in foods, but he was probably less correct in attributing the effect of crude fibre mainly to work of digestion. Recent investigations suggest that the energy cost of digesting even fibrous roughages is quite small and is insufficient to account for the large differences between predicted and actual starch equivalents for foods of this kind. The effect of crude fibre is now

better explained in terms of two phenomena discussed earlier. First, as the fibre content of a food rises, the rumen volatile fatty acid mixture resulting from it contains an increasing proportion of acetic acid. Second, as the acetic acid content of volatile fatty acid mixtures increases, their energy is utilised less efficiently for body fat synthesis.

It is surprising that Kellner should have found digested starch and digested cellulose to be equal in net energy value for fat production, for starch would be expected to give rise to a volatile fatty acid mixture which would be utilised considerably more efficiently than that from cellulose.

TABLE 12.4 Factors for Correcting the Predicted Starch Equivalents of Roughages on the Basis of their Crude Fibre Content

Type of roughage	Crude fibre content (per cent)	Starch equivalent deducted for each 1 per cent of crude fibre
Hay and straw	—	0.58
Chaff	—	0.29
Green fodders	>16	0.58
	14-16	0.53
	12-14	0.48
	10-12	0.43
	8-10	0.38
	6-8	0.34
	4-6	0.29

The Starch Equivalent system is used throughout most of Europe and the British Commonwealth. Kellner's results were used also to supplement those of Armsby in the founding of the American Net Energy system. The Starch Equivalent system has from time to time been modified. Thus T. B. Wood, who included starch equivalents in the first (1921) edition of his bulletin *Rations for Livestock*, increased Kellner's values for roughages by 20 per cent because he found the latter's method of prediction gave values lower than the net energy values found in Armsby. In theory Armsby's values should be higher, because they were determined below maintenance while Kellner's were measured at super maintenance levels. In more recent editions of *Rations for Livestock* the 20 per cent increase has been retained for hays but removed for straws.

The Scandinavian Food Unit System

This system has in common with the two discussed so far the fact that it evaluates foods in terms of the production they promote in the

animal. It differs from Armsby's and Kellner's systems in that foods are evaluated in simple feeding trials and not by calorimetry. In addition, the value of a food is stated not in absolute terms but relative to the value of a common food, barley, and in this respect the Scandinavian Food Unit system resembles the Starch Equivalent system.

The food under investigation is substituted for barley, or for another food of known value, in a control ration, and the original and revised rations are compared with one another in terms of the production they promote in lactating cows or fattening pigs. If it were found, for example, that 1 kg of barley in the ration of a dairy cow could be replaced by 1.2 kg of oats without affecting milk production or body weight change, the oats would be given a value of $1.0/1.2 = 0.83$ food units per kg.

This method of evaluation requires no elaborate apparatus, but is expensive in terms of animals and time. (An experiment to evaluate one food with reasonable accuracy would need 30–40 cows and last 20 weeks.) As in other systems, therefore, the need for laborious experimentation has been avoided by predicting food unit values from the digestible nutrients of foods. The factors used are essentially those of Kellner, except that digestible protein is considered to have a net energy value 1.43 times that of carbohydrate, which is 50 per cent. higher than Kellner's factor of 0.94. The justification for the higher factor is that when foods are given to milking cows and to pigs their protein is used for milk and tissue protein synthesis and is not deaminated, as in Kellner's fattening steers; the losses of energy in urine and as heat which are associated with deamination are therefore reduced.

Total Digestible Nutrients as a Measure of Food Energy

The total digestible nutrients (TDN) content of a food, referred to earlier in Chapter 10, is calculated by adding together the quantities in 100 lb of food of digestible crude protein, crude fibre and nitrogen-free extractives, together with 2.25 times the quantity of digestible ether extract. The barley meal of Table 12.2, which had 12.6 per cent. digestible crude protein, would therefore contain $12.6 + 0.2 + 65.8 + (2.25 \times 1.6) = 82.2$ lb TDN per 100 lb dry matter. In so far as they take into account the higher gross energy content of fat relative to that of carbohydrate (Table 11.1), TDN values provide a relative measure of the digestible energy content of foods. No allowance, however, is made for the higher energy value of protein, which averages 5.65 kcal per g for mixed protein as compared with 4.15 for mixed carbohydrate.

If the amino acids absorbed are deaminated and oxidised, about 20 per cent of their energy is lost in the urine in the form of urea and other by products of protein katabolism. There is therefore less difference between the metabolisable energy values of protein and carbohydrate than between their digestible energy values, and since, in the calculation of TDN, carbohydrate and protein are assumed to be equal in energy, it is sometimes claimed that TDN values are relative measures of metabolisable rather than digestible energy.

From the results of experiments where both TDN and digestible energy values were measured, it has been calculated that on average 1 lb TDN provides approximately 2000 kcal digestible energy (4.4 kcal per g). For ruminants, 1 lb TDN provides about 1600 kcal metabolisable energy.

The TDN system has its origins in the first digestibility trials carried out in the mid nineteenth century, and the present method of calculation was adopted in the early years of the present century. The system has been used in the United States from that time without modification, although there have been suggestions that it should be put on a true digestible energy basis by multiplying digestible crude protein by 1.36.

The Accuracy of the Systems

The purpose of systems for evaluating food energy may be stated in very simple terms. It is to allow the prediction of the energy balance of animals from their food intakes, or—and this amounts to much the same thing—to predict the amount of food required to promote a particular energy balance. Ideally this purpose should be achieved by allotting each food a single energy value, which would be applicable for predicting energy balance in animals of different species, ages and forms of production, and applicable whatever the physical form or quantity of food given or the nature of the other components of the ration. It is recognised that, because there are great differences in digestive physiology between farm animals of different species, no single energy value will be equally appropriate for a food given to ruminants, pigs and poultry, but in all other respects the various energy systems are intended to satisfy the ideal requirements listed above. It is important to assess to what extent these exacting requirements are likely to be met.

Three net energy systems, ostensibly different from one another but in fact interrelated, have now been described, together with the TDN system which is based on digestible and metabolisable energy. (A true metabolisable energy system for ruminants was devised in

Scandinavia but has not been used to any extent.) An important feature of all the systems is that they were devised in the early days of energy metabolism studies, before many of the factors now known to influence energy metabolism had been recognised or understood. Indeed it was often inconsistencies in the systems that were the spur to further experimentation. If the systems are appraised in the light of knowledge acquired since their formulation, certain weaknesses become apparent. These will now be discussed.

The validity of unit values for foods when given to animals with differing forms of production. In all the systems for ruminants, each food is given a single energy value. This suggests that foods supply the same amounts of energy regardless of the purpose for which they are used by the animal, although it was shown in the preceding chapter that such equality is unlikely to prevail. If, for example, hay is given as the sole food to an adult sheep and in quantities insufficient for maintenance, the efficiency with which its metabolisable energy is utilised will be greater than if the same hay is added to a maintenance ration. The metabolisable energy value will be approximately the same in both cases, and therefore the net energy value of the hay will be higher when it is used for maintenance than when it is used for production. The net energy value may be different again if the animal is lactating, or is storing energy principally in body protein rather than in body fat.

When this effect of form of production, i.e. physiological function, on the energy value of a food was recognised, it was considered that the complication it introduced into systems of energy evaluation could be avoided by adjusting the values used to express animal requirements. Suppose foods are evaluated in terms of the net energy they supply when used for body fat synthesis (this net energy may be termed their *net kilocalories for fattening*, or NK_f), and they actually supply 30 per cent. more net energy when used for maintenance. The net energy requirements of animals for maintenance must then be multiplied by $100/(100+30)$ in order to express them in the units used in evaluating foods, i.e. in NK_f .

In fact, Kellner had previously used this adjustment in his system. He stated the requirements of a 1000-lb steer to be, for maintenance, about 5.8 lb SE per day, and for body fat production 4 lb SE per lb of fat; the ratio between these requirements is 1.45:1. More recent estimates of the net energy expended in the maintenance of a 1000-lb steer (8000 kcal per day—see Chapter 14), when coupled with the energy retained in 1 lb of body fat (9.5 kcal per g, or 4300 kcal per lb),

give a ratio of maintenance to production requirement of 8000/4300 or 1.86. The apparent disagreement with Kellner's values is resolved if the latter are converted to net energy. For fattening, as stated previously, 1 lb SE supplies 1071 kcal; hence $4 \times 1071 = 4284$ kcal are required for each lb of fat retained. For maintenance, on the other hand, 1 lb SE supplies 1400 kcal per 1 lb SE; from this the net energy requirement of Kelloer's steer is calculated as $5.8 \times 1400 = 8210$ kcal. The values 4284 and 8210 kcal calculated from Kelloer's values are now in close agreement with the net energy estimates given above.

The same approach is used to allow for differences in net energy value that occur when the same food is used for different forms of production. The experiments referred to earlier (p. 179) on energy utilisation for milk production showed that 1 lb SE promoted the secretion of milk containing 1339 kcal. The quantity of starch equivalent required to produce 1 gallon of milk, containing 3400 kcal, is therefore calculated as $3400/1339 = 2.54$ lb, not $3400/1071 = 3.17$ lb. Animal requirements are weighted in a similar manner in the TDN system.

The success of this solution to the problem posed by foods having different values for different functions depends on whether the relative values for different functions are the same for all foods. In the Starch Equivalent system, the average calorie values of 1 lb starch equivalent are 1400, 1071 and 1339 kcal for maintenance, fattening and milk production respectively, but it is questionable whether these *average* values hold true for individual foods. As described in the previous chapter, the ratio between the efficiency with which metabolisable energy is used for fattening and that when it is used for maintenance tends to be narrower with foods higher in metabolisable energy, and this will be reflected in the ratio between net energy values for the two functions. An example of this effect is given in Table 12.5.

The final column shows that the grasses differ markedly in the ratio of their net energy values for maintenance and for production. The value expected in the final column is 76 per cent, since on average 1 lb starch equivalent supplies 1071 kcal net energy for fattening and 1400 kcal for maintenance, and $100(1071/1400) = 76$. The example shows that individual observations may be a long way from the average. A comparison between the efficiency values of Table 11.5 and those of Table 11.7 suggests that this ratio may vary quite widely. Although little information is available on net energy values for milk production, it seems likely that the ratio of 100/95 between values for maintenance and milk production will also vary.

The conclusion is inescapable that any system of evaluation in which

foods are given single energy values will be an inaccurate system. All the systems now in use come into this category. One would expect that a system like Kellner's, in which foods were evaluated in terms of net energy for body fat synthesis, would tend to underestimate the value for maintenance of low-energy foods such as roughages. In the United Kingdom this tendency has been partly avoided through Wood's 20 per cent. elevation of the starch equivalents of hays, but as a result there is now a tendency in the opposite direction, for the value of roughages for productive purposes to be overestimated. The latter tendency is observed in practice—it has long been the impression

TABLE 12.5. Energy Values (kcal/lb Dry Matter) of Dried Ryegrass for Maintenance and Body Fat Production
(After D. G. Armstrong, 1960, *Proc. 8th int. Grassld Congr.*, p. 485)

Grass	Metabolisable energy	Net energy		(2) as a percentage of (1)
		(1) for maintenance	(2) for fattening	
Young	1400	1113	750	67.4
Mature	1070	789	410	52.0

of farmers and agricultural advisers that 1 lb of starch equivalent in roughages does not promote the same liveweight gain as 1 lb in concentrated foods.

Level of feeding and associative effects. In all energy systems the values assigned to foods are used as if they were additive. It is assumed, first, that in an animal receiving one food only, doubling food intake will also double energy intake, or in other words that the energy value of a food remains the same regardless of the level of feeding. A second assumption made is that the energy value of a ration can be calculated by summation of the energy contributed by each of its component foods. As discussed earlier, there is much evidence that both assumptions are incorrect. The proportion of food energy lost in the excreta is affected both by the quantity of food given and by associative effects between foods. Losses as heat also show associative effects, but are independent of the level of feeding (provided that complications due to energy being utilised for differing functions are taken into account). But in none of the systems now in use are associative and level of feeding effects taken into account.

The prediction of energy value. The net energy value of a food is far from being a constant, even when measured by calorimetry. Yet the values used in practice are, typically, predicted rather than measured,

and are therefore subject to the additional error introduced by the method of prediction. Kellner's Starch Equivalent system was devised from measured values for about 30 foods, of which 10 were roughages. An examination of his results for roughages suggests that their directly determined starch equivalents could be estimated from their digestible nutrients with an accuracy of the order of ± 10 per cent. In simple terms this means that, if a roughage is predicted to have a starch equivalent of 40, there is approximately a 50 per cent chance that the true value lies between 37 and 43 and a 95 per cent chance of it lying between 30 and 50. Accuracy of prediction is doubtless greater for concentrates, for which individual value numbers are used, but even so the accuracy implied by quoting starch equivalents to one decimal place, as is often done, is misleading. Nearly all the values now in use are predicted, not measured, indeed no direct determination of starch equivalent was made in Britain until Kellner's system had been in use for over 30 years.

Present Systems and a New System

There is now much theoretical evidence that the present systems for evaluating food energy are unlikely to be able to achieve their object, the accurate prediction of the effect of food intake on energy balance in animals, and hence on their production. This theoretical evidence has often been confirmed in the practical application of the systems, where the general experience has been that, while all systems are satisfactory for comparing foods not greatly different from one another, they are much less accurate for comparisons between such dissimilar foods as a roughage and a concentrate.

There is probably nothing to choose between the three net energy systems. The TDN system however has the advantage that values can readily be determined by direct measurement, and it is also claimed that the TDN value of a food comes much closer to being a constant than does its net energy value. Since much of the variability in net energy values is attributable to variations in the efficiency of utilisation of metabolisable energy, this is a just claim, but it is a misleading one if considered in relation to the object of the system. The greater stability of TDN values is obtained, not by overcoming the causes of variation in net energy values, but by ignoring them. In other words, it is assumed in the TDN system that for any one function of the animal metabolisable energy will always be used with the same efficiency, whatever the nature of the food. This assumption is not far from the truth as far as the function of maintenance is concerned, but it is quite

incorrect for the various forms of production. Recent American experiments have shown TDN to be less accurate than net energy as a basis for predicting the performance of productive animals.

It seems inescapable that a system which is to describe accurately the relation between food intake and energy balance in ruminants must be one based on net energy. The important questions are how the net energy values of foods should be assessed, and how expressed. In Britain the Starch Equivalent system has come in for much criticism in recent years, and as a result a new system to replace it has been proposed by K. L. Blaxter. This system was described originally in Blaxter's book (see 'Further Reading' at end of this chapter), but has since been modified slightly. The version described below includes these modifications.

The new system attempts to combine the better features of both metabolisable and net energy systems. The energy values of foods are expressed in terms of metabolisable energy, and the metabolisable energy value of a ration is calculated by adding up the metabolisable energy contributed by its constituents. Associative effects on metabolisable energy are therefore ignored.

For an example of the system, we may consider a 300-kg steer fed on a daily ration of 5 kg hay and 2 kg maize. This would supply the following quantities of metabolisable energy.

Food	Quantity (kg/day)	Metabolisable energy in food supplied	
		(Mcal/kg)	(Mcal/day)
Hay	5	1.90	9.50
Maize	2	3.30	6.60
			<hr/> 16.10

If the food contains 90 per cent dry matter, the concentration of metabolisable energy in the dry matter would be $16\frac{1}{7} \times 0.9 = 2.55$ Mcal/kg. This concentration (designated *M/D*) is important in later calculations.

When the total metabolisable energy supplied by the ration has been determined, the next step is to calculate the quantity of metabolisable energy needed by the animal for maintenance. The efficiency with which metabolisable energy is used in providing energy for maintenance is reasonably constant, and it is often permissible to assume an average value of 74 per cent. The quantity of metabolisable energy required

may then be calculated by multiplying the fasting metabolism of the animal by $100/74 = 1.35$. For more exact calculations, the efficiency of utilisation of metabolisable energy for maintenance (k_m) may be predicted from the metabolisable energy concentration of the ration (M/D). An equation for predicting k_m in this way is

$$k_m = 6.8 M/D + 54.6$$

(where M/D = Mcal metabolisable energy per kg dry matter)

For our example, k_m is 72. The fasting metabolism of a 300 kg steer is 6.75 Mcal/day, and hence its maintenance requirement for metabolisable energy is

$$6.75 \times 100/72 = 9.38 \text{ Mcal/day.}$$

Before the metabolisable energy surplus to that required for maintenance is considered, a correction must be made for the effect of level of feeding (see p. 161). To make this correction the total metabolisable energy of the ration is multiplied by a factor f , which varies according to the level of feeding and the metabolisable energy concentration (M/D). The formula for f is

$$f = 1 - \frac{0.418 \Delta L}{M/D} + 0.11 \Delta L$$

(where ΔL = increase in feeding level over maintenance)

In the example, $M/D = 2.55$ and $L = 16.10/9.38 = 1.72$, ΔL is therefore 0.72. With these values f is calculated to be 0.961, and the corrected metabolisable energy supplied by the ration is $16.10 \times 0.961 = 15.47$ Mcal/day.

Subtracting the metabolisable energy required for maintenance from the total corrected metabolisable energy in the ration gives the quantity available for production ($15.47 - 9.38 = 6.09$ Mcal/day). In a fattening animal the efficiency with which this is utilised (k_f) will vary over a wide range according to the nature of the ration, and must therefore be predicted from M/D . A suitable equation is

$$k_f = 18.4 M/D + 3.0,$$

which gives a value of 50 for the ration under consideration. This equation is intended to apply for both immature growing animals and mature fattening animals. For milk production the efficiency of utilisation of metabolisable energy does not vary much from 70 per cent (see Chapter 15).

The energy retained by the animal is calculated by multiplying the metabolisable energy surplus to the maintenance requirement by

$k_f/100$. In our example, energy retention is

$$6.09 \times 50/100 = 3.04 \text{ Mcal/day.}$$

Finally, the energy retention of the animal is translated into liveweight gain by dividing it by the estimated energy content of the gain. In this example, a value of 3 Mcal/kg gain is assumed, and liveweight gain would be

$$3.04/3 = 1.01 \text{ kg/day.}$$

This new system takes into account nearly all the major factors known to affect the utilisation of food energy. The only significant factor not considered is that of associative effects on metabolisable energy values. The system is also intended to be sufficiently flexible to incorporate any further factors which come to light.

The chief drawback of Blaxter's system is that in rationing animals it does not allow the simple balancing of net energy supply and net energy requirements which is a feature of the Starch Equivalent system. The new system is intended for use in predicting the animal performance obtainable with particular rations, and its use in the reverse manner, namely to determine how much food is needed to achieve a particular level of production in the animal, involves an iterative procedure. The second disadvantage is that the system achieves the greater accuracy it is likely to have only at the expense of simplicity. Both disadvantages can to some extent be overcome by expressing the calculations in a graphical form.

ENERGY SYSTEMS FOR PIGS AND POULTRY

In the feeding of pigs and poultry, less emphasis is placed upon the energy content of the food than in feeding ruminants. The main reason for this is that pigs and poultry, because they digest cellulose to only a small extent, are limited to a range of foods varying comparatively little in energy content. Nevertheless net energy systems have been developed for evaluating both pig and poultry foods, although they have not been used much in practice.

Pigs

Fingerling, who was Kellner's successor at the Mückern Experiment Station, carried out a large number of starch equivalent determinations with pigs. His results, however, are not in general use, and the energy values of foods for pigs are generally stated in terms of metabolisable

energy, TDN or digestible energy. It is considered that the metabolisable energy of the foods commonly given to pigs is utilised with approximately the same efficiency for any particular function of the animal. Fingerling's results, some of which are given in Table 11.7, suggest that, although the metabolisable energy in the foods of pigs is used with less variable efficiency than is that in the foods of ruminants, there is still appreciable variability. It seems unlikely, however, that in the future there will be any move away from digestible or metabolisable energy to net energy as a basis for evaluating the energy of pig foods.

Poultry

Net energy values of foods for poultry were determined in the United States by Fraps, who used the method of comparative slaughter to measure energy retention in young chickens. The figures obtained were called *productive energy* values, in order to emphasise that they were net energy values for growth, not maintenance. Fraps also devised methods for predicting the productive energy values of foods from their gross or digestible nutrients.

Fraps's productive energy values have not been used much in the United Kingdom. As for pig foods, it is argued that for most poultry foods metabolisable energy is used with reasonably constant efficiency, and therefore that metabolisable energy is as satisfactory a basis for evaluation as net or productive energy. The work of Fraps has been criticised on the grounds, first, that the comparative slaughter technique is insufficiently accurate to give reliable results, and second, that even if net energy values could be measured accurately they would still show those inconsistencies caused by associative effects of foods, by the form in which energy is stored by the animal, and so on, which are so apparent in net energy values for ruminants. If the last criticism is valid, it is difficult to see how metabolisable energy could serve as a reliable means for predicting energy retention in poultry. But since Fraps's results show certain inconsistencies, they do not provide a serious challenge to the view now widely held that metabolisable energy is a satisfactory basis upon which to evaluate poultry foods. It is surprising that so little calorimetry has been carried out with poultry, only two determinations of the efficiency of utilisation of metabolisable energy having been reported for poultry foods. The results of these, given in Table 11.7, do not conflict with the constant efficiency commonly assumed.

In both the United Kingdom and the U.S.A. it has been decided

that the energy value of poultry foods should be expressed as metabolisable energy. Metabolisable energy is very easily measured in poultry—it is in fact easier to determine than digestible energy, because faeces and urine are voided together. In addition there are reliable methods for predicting the metabolisable energy of the more common poultry foods from their chemical composition.

FURTHER READING

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THE EVALUATION OF FOODS

(D) PROTEIN

Proteins are made up of amino acids, the classification of which into essential and non essential has already been described in Chapter 4, and in Chapter 9 under 'Protein Synthesis'. For food to be used with maximal efficiency the animal must receive the essential amino acids in the correct quantities, and sufficient of the non essential amino acids to meet the metabolic demands must also be available. Simple-stomached animals such as pigs and poultry obtain these acids from the breakdown of proteins during digestion and absorption, whereas in ruminant animals the position is more complex. Considerable degradation and synthesis of protein occur in the rumen, so that the material which finally becomes available for digestion by the animal differs considerably from that originally present in the food. Different approaches to the evaluation of protein sources are therefore necessary for ruminant and for non ruminant animals.

At first foods were evaluated as sources of protein by rather crude and simple methods, which took no account of the species of animal for which the foods were intended. These methods are still in use and will be dealt with first, and then the more refined methods of assessing protein quality will be discussed for simple stomached and ruminant animals separately.

Crude protein (CP) Most of the nitrogen required by the animal is used for protein synthesis. Most of the food nitrogen also is present as protein, and it is convenient and almost universal for the nitrogen requirements of animals and the nitrogen status of foods to be stated in terms of protein. Chemically the protein of a food is calculated from its nitrogen content, determined by a modification of the classical Kjeldahl technique, this gives a figure for nitrogen in all forms except nitrate and nitrite nitrogen. Two assumptions are made in calculating the protein content from the nitrogen: firstly, that all food protein contains 16 per cent of nitrogen, and secondly, that all the nitrogen of the food is present as protein. The percentage of nitrogen (N) is then expressed in terms of crude protein (CP), calculated as follows

$$\text{per cent CP} = \text{per cent N} \times 100/16,$$

or more commonly

$$\text{per cent. CP} = \text{per cent. N} \times 6.25.$$

Both of these assumptions are unsound. Different food proteins have different nitrogen contents, and therefore different factors should be used in the conversion of nitrogen to protein for individual foods. Table 13.1 shows the nitrogen content of a number of common proteins together with the appropriate nitrogen conversion factors. Although fundamentally unsound, the use of an average conversion factor of

TABLE 13.1. Factors for Converting Nitrogen to Crude Protein
(From D. B. Jones, 1931, U.S.D.A. Circ. 183)

<i>Food protein</i>	<i>Per cent. nitrogen</i>	<i>Conversion factor</i>
Cottonseed	18.87	5.30
Soya bean	17.51	5.71
Barley	17.15	5.83
Maize	16.00	6.25
Oats	17.15	5.83
Wheat	17.15	5.83
Egg	16.00	6.25
Meat	16.00	6.25
Milk	15.68	6.38

6.25 for food proteins is considered to be justified in practice—except that where a single food provides the major part of the protein of the diet, the error resulting from the use of this factor could be of importance, especially with certain of the oilseed residues. The assumption that the whole of the food nitrogen is present as protein is also false, since many simple nitrogenous compounds such as amides, amino acids, glycosides, alkaloids, ammonium salts and compound lipids may be present (see Chapter 4). Quantitatively however only the amides and amino acids are important, and these are present in large amounts in only a few foods, such as young grass, silage and immature root crops. In the diets of pigs and poultry, cereals and oilseed meals predominate, and in these there is little non-protein nitrogen. Hence in practice there is little to be gained from attempting to distinguish between the two types of nitrogen, particularly as a considerable proportion of the non-protein fraction can be utilised for amino acid synthesis by the animal.

True protein (TP). Where true protein needs to be determined, it can be separated from non-protein nitrogenous compounds by precipitation with cupric hydroxide, or in some plant material by heat

coagulation. The protein is then filtered and the residue subjected to a Kjeldahl determination.

Digestible crude protein (DCP) The crude protein figure provides a measure of the nitrogen present in the food, but gives little indication of the usefulness of this nitrogen to the animal. Before the food becomes available to the animal it must undergo digestion, during which it is broken down to simpler substances which are absorbed into the body. The digestible protein in a food may be determined by digestibility trials, as described in Chapter 10. Such trials give figures for 'apparent' and not 'true' digestibility owing to the presence in the faeces of metabolic nitrogen, which is not derived directly from the food but from wastage in the animal's body. The apparent figures are thus lower than the true values, but since the loss of metabolic faecal nitrogen is inevitable they are a more realistic measure of nutritive value. Usually no attempt is made to determine the true digestibility, and the coefficients in everyday use are apparent values.

Protein digestibility is sometimes estimated by incubating the food with acid pepsin for 48 hours at 37°C. The protein content of the insoluble residue is then estimated by the Kjeldahl method, and the digestible protein calculated by subtracting this value from the protein content of the food. The method is of very limited value, since it involves the action of only one enzyme instead of the many of the digestive tract, and also varies with fineness of grinding and conditions of drying of the food. At best it may be useful for comparative purposes.

MEASURES OF PROTEIN QUALITY FOR SIMPLE STOMACHED ANIMALS

Digestible protein figures are not entirely satisfactory assessments of a protein because the efficiency with which the absorbed protein is used differs considerably from one source to another. In order to take this into account methods of evaluating proteins have been devised which are based on the response of experimental animals to the protein under consideration.

Protein efficiency ratio (PER) The protein efficiency ratio normally uses growth of the rat as a measure of the nutritive value of dietary proteins. It is defined as the weight gain per unit weight of protein eaten and may be calculated by using the following formula

$$\text{PER} = \frac{\text{gain in body weight (g)}}{\text{protein consumed (g)}}$$

The value varies with the level of protein intake, and is at a maximum for different proteins at different levels. Determining which level of intake is associated with the maximum PER enables a comparison of the quality of different protein sources to be made. A modification, where the weight gain compared with that of a control group fed on a protein-free ration is divided by the protein consumed, gives the *net protein ratio* (NPR).

Gross protein value (GPV). The liveweight gains of chicks receiving a basal diet containing 8 per cent. crude protein are compared with those of chicks receiving the basal diet *plus* 3 per cent. of a test protein, and of others receiving the basal diet *plus* 3 per cent of casein. The extra liveweight gain per unit of supplementary test protein, stated as a percentage of the extra liveweight gain per unit of supplementary casein, is the gross protein value of the test protein, i.e.

$$\text{GPV} = \frac{A}{A_0} \times 100,$$

where A is g increased weight gain/g test protein, and A_0 is g increased weight gain/g casein.

Determinations of the PER, NPR or GPV require a regular supply of standard young animals, which have to be looked after individually during the experimental period. Thus these methods of protein evaluation are expensive and require considerable technical resources. The most commonly used is the GPV, but this is limited in its usefulness, since it provides information only on the relative value of a protein in supplementing a particular basal ration; in addition it depends upon measurement of liveweight gains which may not be related to protein stored. A more accurate evaluation of protein may be obtained by using the results of nitrogen balance experiments. In such experiments the nitrogen consumed in the food is measured as well as that voided in the faeces, urine and any other nitrogen-containing product such as milk, wool or eggs. Where the nitrogen intake is equal to the output, the animal is in nitrogen equilibrium. Where the intake exceeds the output, it is in positive nitrogen balance. Where output exceeds intake, the animal is in negative balance. Table 13.2 illustrates the calculation of a nitrogen balance for a 42-kg pig fed on a diet containing soya bean meal as the protein source. The pig was in positive nitrogen balance, storing 10.77 g nitrogen per day.

Protein replacement value (PRV). This value measures the extent to which a test protein will give the same balance as an equal amount of a standard protein. Two nitrogen balance determinations are carried

out, one for a standard such as egg or milk protein, which is of high quality, and one for the protein under investigation. The PRV is calculated as follows

$$\text{PRV} = \frac{A-B}{N \text{ intake}}$$

where A = N balance for standard protein in mg per basal kcal,
 B = N balance for protein under investigation in mg per basal kcal
 The method can also be used to compare two proteins under similar conditions, where no standard value for replacement is required

TABLE 13.2 Nitrogen Balance for a Hampshire Pig on a Soya Bean Meal Diet
 (From D. G. Armstrong and H. H. Mitchell, 1955 *J. Anim. Sci.*, 14, 53)

	Daily intake (g)	Daily outgo (g)
Food nitrogen	19.82	—
Faecal nitrogen	—	2.02
Urinary nitrogen	—	7.03
Nitrogen retained by the body	—	10.77
	19.82	19.82

Balance = +10.77 g/day

The PRV measures the efficiency of utilisation of the protein given to the animal. Other methods measure the utilisation of digested and absorbed protein.

Biological value (BV) This is a direct measure of the proportion of the food protein which can be utilised by the animal for synthesising body tissues and compounds, and may be defined as the percentage of the nitrogen absorbed which is retained by the animal. A balance trial is conducted in which nitrogen intake and urinary and faecal excretions of nitrogen are measured, and the results are used to calculate the biological value as follows

$$\text{BV} = \frac{N \text{ intake} - (\text{faecal N} + \text{urinary N})}{N \text{ intake} - \text{faecal N}} \times 100$$

Part of the nitrogen of the faeces, however, the *metabolic faecal nitrogen*, is not derived directly from the food. Urinary nitrogen also contains a portion of nitrogen, known as the *endogenous urinary nitrogen*, which is not directly derived from food nitrogen. The significance of the endogenous urinary nitrogen is discussed in more detail later (Chapter 14). Briefly, it is nitrogen derived from expendable tissues and secretions, together with waste nitrogen arising during normal catabolism and resynthesis of tissue proteins. The existence in both faeces

and urine of nitrogen fractions whose excretion is independent of food nitrogen is most convincingly demonstrated by the fact that some nitrogen is excreted when the animal is given a nitrogen-free diet. Such diets, adequate in all other respects, provide a means of measuring the magnitude of endogenous urinary nitrogen and metabolic faecal nitrogen (see Chapter 14). Since both fractions represent nitrogen which has been utilised by the animal rather than nitrogen which cannot be utilised, it is obvious that their exclusion from the faecal and urinary fractions in the formula given above will yield a more precise estimate of biological value. The revised formula is

$$BV = \frac{N \text{ intake} - (\text{faecal N} - \text{MFN}) - (\text{urinary N} - \text{EUN})}{N \text{ intake} - (\text{faecal N} - \text{MFN})} \times 100$$

where MFN = metabolic faecal nitrogen and EUN = endogenous urinary nitrogen.

'Biological values' are normally calculated by this equation, while those derived from the former equation are usually termed 'apparent biological values'. In determining biological value, as much as possible of the dietary protein should be provided by the protein under test. Protein intake must be sufficient to allow adequate nitrogen retention, but must not be in excess of that required for maximum retention; if the latter level were exceeded, the general amino acid katabolism resulting would depress the estimate of biological value. For the same reason sufficient non-nitrogenous nutrients must be given to prevent katabolism of protein to provide energy. The diet must also be adequate in other respects. Table 13.3 shows an example of the calculation of a biological value from nitrogen balance data, and in Table 13.4 biological values are given for the proteins of some typical foods.

Such biological values are for the combined functions of maintenance, meaning the replacement of existing proteins, and growth, or the formation of new tissues. A biological value for maintenance alone may be calculated from nitrogen balance data. A linear relationship exists between nitrogen intake and nitrogen balance below equilibrium (Fig. 14.2) which is represented by the following equation:

$$y = bx - a,$$

where y = nitrogen balance,	} mg nitrogen per basal kcal;
x = nitrogen absorbed,	
a = nitrogen loss at zero intake	

b , the nitrogen balance index, represents that fraction of the absorbed

nitrogen which is retained in the body, and when expressed as a percentage is equal to the biological value

The usefulness of a protein to the animal will depend upon its digestibility as well as its biological value. The product of these two values

TABLE 13.3 Calculation of Biological Value of a Protein for Maintenance and Growth of the Rat
(After H. H. Mitchell, 1924, *J. biol. Chem.*, 58, 873)

Food consumed daily (g)	6.00
Nitrogen in food (per cent.)	1.043
Daily nitrogen intake (mg)	62.6
Total nitrogen excreted daily in urine (mg)	32.8
Endogenous nitrogen excreted daily in urine (mg)	22.0
Total nitrogen excreted daily in faeces (mg)	20.9
Metabolic faecal nitrogen excreted daily (mg)	10.7

$$BV = \frac{62.6 - (20.9 - 10.7) - (32.8 - 22.0)}{62.6 - (20.9 - 10.7)} \times 100$$

$$= 79$$

is the proportion of the nitrogen intake which is retained, and is termed the *net protein utilisation* (NPU). The product of the NPU and the percentage crude protein is the *net protein value* (NPV) of the food, and is a measure of the protein actually available for metabolism by the animal.

TABLE 13.4 Biological Values of the Protein in various Foods for Maintenance and Growth for the Growing Pig
(From D. G. Armstrong and H. H. Mitchell, 1955, *J. Anim. Sci.*, 14, 53)

Food	BV
Milk	95-97
Fish meal	74-89
Soya bean meal	63-76
Cottonseed meal	63
Linseed meal	61
Maize	49-61
Barley	57-71
Peas	62-65

The amino acid mixtures absorbed by the animal are required for the synthesis of body proteins. The efficiency with which this synthesis can be effected depends partly on how closely the amino acid proportions of the absorbed mixture resemble those of body proteins, and partly on the extent to which these proportions can be modified. The biological value of a food protein, therefore, depends upon the number and kind of amino acids present in the molecule: the nearer the food

protein approaches the body proteins in amino acid make-up, the higher will be the biological value. Animals have little ability to store amino acids in the free state, and if an amino acid is not immediately required for protein synthesis it is readily broken down and either transformed into a non-essential amino acid which is needed by the animal, or used as an energy source. Since essential amino acids cannot be effectively synthesised in the animal body, an imbalance of these in the diet leads to a wastage. Food proteins with either a deficiency or an excess of any particular amino acid will tend to have a low biological value.

If we consider two food proteins, one deficient in lysine and rich in methionine and the other deficient in methionine but containing an excess of lysine, then if these proteins are given separately to young pigs, they will both have low biological values because of the imbalance of these two essential amino acids. If however the two proteins are given together, then the mixture of essential amino acids will be better balanced and the mixture will have a higher biological value than when either protein is given alone. Such proteins supplement each other. In practice, and for a similar reason, it often happens that a diet containing a large variety of proteins has a higher biological value than a diet containing only a few. This also explains why biological values for individual foods cannot be applied when mixtures of foods are used, since clearly the resultant biological value of a mixture is not simply a mean of the individual components. For the same reason it is impossible to predict the value of a protein, as a supplement to a given diet, from its biological value.

Animal proteins generally have higher biological values than plant proteins, although there are exceptions such as gelatine, which is deficient in several essential amino acids.

The amino acid composition of a given food protein will be relatively constant (see Appendix Table 4), but that of the protein to be synthesised will vary considerably with the type of animal and the various functions it has to perform. For the normal growth of rats, for example, lysine, tryptophan, histidine, methionine, phenylalanine, leucine, isoleucine, threonine, valine and arginine are dietary essentials. Man does not require histidine, while chicks need glycine as well as those required by the rat to ensure normal growth. On the other hand arginine is not a dietary requirement for maintenance of the rat.

The situation is further complicated by the fact that some amino acids can be replaced in part by others; for example methionine can partly be replaced by cystine, and similarly tyrosine can partly replace

phenylalanine. In such cases the two amino acids are frequently considered together in assessing the animal's requirements. It is obvious that no single figure for biological value will suffice as a measure of the nutritive value of a food protein for different animals and different functions. The difference in amino acid requirements for young pigs compared with those for laying hens, for example, is shown in the Appendix Tables 10 and 11. The consequent need for multiple figures limits the use of the biological value concept in practice.

Since biological value is dependent primarily upon essential amino acid make-up, it would seem logical to assess the nutritive value of a protein by a quantitative estimation of its essential amino acid constitution and then compare this with the known amino acid requirements of a particular class of animal, such analyses of food proteins may be readily carried out by modern applications of chromatographic techniques. Evaluations of proteins made by dealing with each amino acid individually, however, would be laborious and inconvenient, and several attempts have been made to state the results of amino acid analyses in a more useful and convenient form.

Chemical score In this concept it is considered that the quality of a protein is decided by that essential amino acid which occurs in it which is in greatest deficit when compared with a standard in the form of egg protein. The content of each of the essential amino acids of a protein is expressed as a percentage of the standard, the lowest percentage being taken as the score. In wheat protein, for example, the essential amino acid in greatest deficit is lysine. The contents of lysine in egg and wheat proteins are 7.2 per cent and 2.7 per cent respectively, and the chemical score for wheat protein is therefore $2.7/7.2 \times 100 = 37$. Such values correlate well with the biological values for rats and human beings but not for poultry. They are useful for grouping proteins into categories, but suffer a serious disadvantage in that no account is taken of the deficiencies of acids other than the acid in greatest deficit.

The essential amino acid index (EAAI) Here the amounts of all the ten essential amino acids present are considered. It may be defined as the geometric mean of the egg ratios of these acids, and is calculated as

$$\text{EAAI} = \sqrt[n]{\frac{100a}{a_e} \times \frac{100b}{b_e} \times \frac{100c}{c_e} \times \dots \times \frac{100j}{j_e}}$$

where a, b, c, \dots, j = percentages of the essential amino acids in the food protein, $a_e, b_e, c_e, \dots, j_e$ = percentages of the same essential amino acids in egg protein, and n = the number of amino acids entering into the calculation.

The index has the advantage of predicting the effects of supplementation in combinations of proteins. It has the disadvantage that proteins of very different amino acid composition may have the same or a very similar index.

Both the chemical score and the essential amino acid index are based upon gross amino acid composition. A more logical approach would be to use figures for the amino acids available to the animal. Such figures may be obtained in several ways. *In vivo* determinations involve amino acid analyses of food and faeces. The figures so obtained are suspect because the faeces contain varying amounts of amino acids not present in the food, and also because digestibility is not synonymous with availability; in addition *in vivo* digestibility trials are laborious and time-consuming and require considerable technical resources and skill. *In vitro* digestibility determinations involve the action of one or at most a few enzymes and are thus not strictly comparable with the *in vivo* action, which involves a series of enzymes—although there is a relationship between the two.

Microbiological assay of available amino acids. Certain strains of *Streptococci* and *Tetrahymena* have proteolytic activity and an amino acid requirement similar to that of domestic animals performing various functions. Such organisms could be used for available amino acid assay by measuring the growth response of a micro-organism to an intact protein in a culture medium deficient in a particular essential amino acid. Recent work with *Streptococcus zymogenes* indicates that it may form the basis of a rapid simple laboratory test for several essential amino acids.

Biological methods. These are based on measuring the growth or nitrogen retention of animals fed on an intact protein as a supplement to a diet deficient only in the amino acid under investigation. The chick is the usual experimental animal, and response to the test material is compared with the responses obtained with supplements of pure amino acids. The construction of diets deficient in specific amino acids but otherwise adequate is one of the main problems. A method for methionine and cystine is operative and has given good results.

Chemical methods. It would be ideal if simple chemical procedures could be used to determine the availability of amino acids, provided the results correlated well with those of accepted biological methods. So far only one promising method has been developed, that for available lysine. The availability of dietary lysine depends upon the extent to which the ϵ -amino groups are not chemically bound. The free ϵ -amino groups of lysine react with fluoro-2,4-dinitrobenzene to

produce a coloured derivative, and this reaction can therefore be used to estimate the lysine with free ϵ -amino groups, i.e. the available lysine. In practice the method has been found to correlate well with biological procedures in evaluating proteins as supplements to diets where lysine is limiting, such as those containing high proportions of cereals. The correlation with biological procedures is also good on all animal-protein diets, even though the sulphur-containing amino acids are usually limiting in this case. With vegetable-protein and high-carbohydrate diets the method is not so satisfactory, the results obtained being too low because of the destruction of the coloured lysine derivative. Various modifications of technique have been proposed to counter this, but none has been completely satisfactory.

Measures of Food Protein used in the Practical Feeding of Pigs and Poultry

The difficulties in assessing the value of proteins in the diet will by now be apparent from the variety of methods that have been proposed,

TABLE 13.5 Relationships between Gross Protein Value and Available Lysine
(From A. W. Boyne *et al.*, 1961, *J. Sci. Fd. Agric.*, 12, 832)

Food		GPV	Available lysine (g/16 g nitrogen)
Fish meal	1	62	3.6
	2	106	5.6
	3	121	6.7
Whale meat meal	1	50	3.7
	2	87	5.0
	3	114	6.7
Meat and bone meal	1	39	2.7
	2	66	4.1
	3	91	4.4

all of which have considerable limitations. A crude protein figure is useful, and this is normally used in preference to digestible crude protein, because the digestibility of the proteins in foods commonly given to pigs and poultry is fairly constant and because the total nitrogen content is readily determined in the laboratory.

The quality of the proteins in a particular food is indicated by stating the contents of all the essential amino acids, or only of those most likely to be deficient. In practice pig and poultry diets are based largely on cereals, and assessment of the protein value of foods for such animals is then a question of measuring their ability to supplement

the amino acid deficiencies of the cereals. The main deficiency in such cases is that of lysine and methionine, so that the most useful measures of protein quality are those which reflect the available lysine or methionine content of the food. The determination of available lysine is now accepted as a routine procedure for animal protein foods in many laboratories.

The gross protein value is the most commonly used biological method for evaluating proteins. Gross protein values measure the ability of proteins to supplement diets consisting largely of cereals, and they correlate well with available lysine figures, as shown in Table 13.5.

RUMINANT ANIMALS

Proteins in foods for ruminant animals are traditionally evaluated in terms of crude protein or digestible crude protein. Realisation that the crude protein fraction contained variable amounts of non-protein nitrogen led to the use of true protein instead of crude protein, but this was unsatisfactory since no allowance was made for the nutritive value of the non-protein nitrogen fraction. The concept of *protein equivalent* (PE), introduced in 1925, was an attempt to overcome this difficulty by allowing the non-protein nitrogen fraction half the nutritive value of the true protein. It was calculated as follows:

$$PE = \% \text{ Digestible TP} + \frac{\% \text{ Digestible CP} - \% \text{ Digestible TP}}{2}$$

or

$$PE = \frac{\% \text{ Digestible CP} + \% \text{ Digestible TP}}{2}$$

Protein equivalent is still widely used, but in the light of present-day concepts of rumen function there seems to be no justification for its use in preference to digestible crude protein (DCP). This is nowadays the most widely used general measure for evaluating protein sources for ruminants.

MEASURES OF PROTEIN QUALITY FOR RUMINANTS

The assessment of protein quality for ruminants is difficult since the food proteins are drastically altered in the rumen by the action of micro-organisms, as described in Chapter 8. Proteins are broken down to amino acids or ammonia and a large proportion of them used for the synthesis of microbial proteins, which are eventually digested and absorbed from the small intestine by the host. The rumen micro-organisms are capable of synthesising all the essential as well as

the non essential amino acids, hence the mixture of amino acids eventually entering the animal's blood bears no relationship to the amino acid make up of the original diet

The biological value of microbial protein is comparatively high, about 80, and clearly the conversion of food protein to microbial protein will in many cases be of advantage to the host. Unfortunately the overall biological value of the food protein is generally less than this value, because of the formation of ammonia in the rumen. Although some ammonia in the rumen is utilised by the micro-organisms, a large amount is absorbed into the blood, where it is converted into urea. Some of this is passed back into the rumen in saliva, but the major part is excreted in the urine. The biological value of proteins for ruminants thus depends largely upon the extent to which ammonia is formed and utilised in the rumen. This in turn depends upon the susceptibility of the protein to deamination and upon the availability of a source of energy for the rumen micro-organisms.

The efficiency of protein synthesis by the rumen micro-organisms depends upon conditions in the rumen, and is increased by diets of low protein content but of a high energy level in the form of soluble carbohydrate. Neither of these latter is a measurable function of the protein source itself, but rather of the diet of which it forms part, so that they cannot be taken into account in an evaluation of a food protein in isolation.

On the other hand the extent to which deamination of food protein takes place depends on such factors as surface area of protein available for microbial attack, physical consistency of the protein, protective action of other constituents, and the chemical nature of the protein. Susceptibility to deamination is thus a property of the protein itself and should be included in a system of protein evaluation.

Measurement of ruminal ammonia concentration An estimate of susceptibility to deamination may be made by measuring the concentration of ammonia in the rumen when the protein is given under standard conditions. The higher the concentration, the greater is the susceptibility.

Measurement of salt peptisability This method is also used for estimating the susceptibility of a protein to deamination, and is carried out by measuring its solubility in a salt solution of standard concentration under standard conditions of time and temperature.

Both these methods involve simple laboratory techniques, but they are not used a great deal in practice because they measure susceptibility to deamination only indirectly.

Measures of Food Protein used in Practical Feeding

Nitrogen balance determinations give the most accurate measures of the value of proteins in given diets. These, however, relate only to the animals and experimental rations used. To cover all possible variations of diet, animal and physiological state is virtually impossible, and even to provide sufficient information to allow of modified application to individual cases would require an enormous amount of work. Such information, should it become available, would be of great value.

At present, evaluation of food protein for ruminants in feeding practice is based on determining the crude protein figure, for which a digestibility coefficient, available from published work, is then assumed and used to calculate a figure for digestible crude protein. Little attempt is made to take the quality of the protein into account in terms of its biological value, since many workers consider that for practical purposes it may be assumed that food nitrogen reaches the abomasum largely as microbial protein, and is thus of constant biological value. This value is sometimes taken into account in formulating protein requirements, and foods may then be evaluated in terms of digestible crude protein. The danger inherent in this approach is illustrated by figures as divergent as 60 and 75 which have been suggested by different workers as the biological value to be assumed.

Food protein cannot be evaluated in isolation but must be considered in relation to the diet as a whole, and in particular to the level of protein and soluble carbohydrate present.

FURTHER READING

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FEEDING STANDARDS FOR MAINTENANCE AND GROWTH

Statements of the amounts of nutrients required by animals are described by the general term, *feeding standards*. Two other terms used in the same context are *nutrient requirement* and *allowance*. Neither is strictly defined, but a rough distinction between them is that, if the requirement is a statement of what animals on average require for a particular function, the allowance is greater than this amount by a safety margin designed principally to allow for variations in requirement between individual animals.

Feeding standards may be expressed in quantities of nutrients or in dietary proportions. Thus the phosphorus requirement of a 50 lb pig might be stated as 7.3 g P per day or as 0.5 per cent P in the diet. The former method of expression is used mainly for animals given exact quantities of foods, the latter for animals fed to appetite. Various units are used for feeding standards. For example, the energy requirements of ruminants may be stated in terms of starch equivalent (net energy), metabolisable energy or TDN, and their protein requirements in terms of available protein, digestible crude protein or, occasionally, crude protein. It is obviously essential that the units used in the standards should be the same as those used in the evaluation of foods. Standards may be given separately for each function of the animal or as overall figures for the combined functions. The requirements of dairy cows, for example, are given separately for maintenance and for milk production, but those for growing chickens are for maintenance and growth combined. In some cases the requirements for single functions are not known: this is true particularly of vitamin and trace element requirements.

As mentioned above, the translation of a requirement into an allowance which is to be used in feeding practice is accompanied by the addition of a safety factor. The justification for such safety factors is illustrated by the following example. Suppose that in cattle of 1000 lb liveweight the requirement for energy for maintenance is found to range in individuals from 5.0 to 6.0 lb starch equivalent, with a mean

value of 5.5 lb. While some of the variation may be caused by inaccuracies in the methods of measurement used, much of it will undoubtedly reflect real differences between animals. This being so, the adoption of the mean estimate of requirement, 5.5 lb SE, as the allowance to be used in practice, will result in some cattle being over- and others underfed. Underfeeding is regarded as the greater evil, and so a safety factor may be added to the requirement when calculating the allowance to be recommended. This safety factor will be designed to ensure that no animals, or only those with an exceptionally high requirement, will be underfed. It may be an arbitrary addition or, better, one based mathematically on the expected variation between animals; the larger this variation, the greater should be the safety factor. Safety factors have been criticised on the grounds that overfeeding, say, 90 per cent. of the population to ensure that the remaining 10 per cent. are not grossly underfed is a wasteful procedure.

Variations between animals, and also between samples of a food, must always be borne in mind when applying feeding standards. Such variations mean that the application of standards to individual animals and individual samples of foods must inevitably be attended by inaccuracies. For this reason feeding standards should be considered as guides to feeding practice, not as inflexible rules; they do not replace the art of the stockman in the finer adjustment of food intake to animal performance. Feeding standards, however, are not restricted in application to feeding individual animals: they can be used on a larger, farm scale to calculate, for example, the total winter feed required by a dairy herd, and even on a national scale to assist in planning food imports.

The object in this chapter and the next will be to discuss the scientific basis for feeding standards and to describe briefly how they are determined. Some tables of feeding standards are included in the Appendix, but as the standards used in the United Kingdom are now being revised, those given in the tables (except those for poultry) must be regarded as interim values. For many years the standards used in the United Kingdom have been contained in the Ministry of Agriculture's bulletins *Rations for Livestock* and *Poultry Nutrition*. (Many other countries have similar publications. The standards used in the United States are summarised in a series of booklets published by the National Research Council, U.S.A., under the general title 'Nutrient Requirements of Domestic Animals'.) In Britain there is a widespread feeling that the standards now in use need to be revised and extended. Some modifications were suggested at a conference held in 1958, and since

then the Agricultural Research Council has set up a committee to review feeding standards. This committee is to publish its findings in technical reviews and summaries for each of the main classes of farm animal. At the time of writing (Spring 1965) only a 'Summary of Recommendations' for poultry has been published.* The interim standards given at the end of the present book are derived from a number of sources, a full list of which is given in the Appendix.

FEEDING STANDARDS FOR MAINTENANCE

An animal is in a state of maintenance when its body composition remains constant, when it gives rise to no product such as milk and when it performs no work on its surroundings. As farm animals are rarely kept in this non-productive state, it might seem to be only of academic interest to determine nutrient requirements for maintenance; but the total requirements of several classes of animals, notably dairy cows, are arrived at factorially by summing requirements calculated separately for maintenance and for production. Consequently a knowledge of the maintenance needs of animals is of practical as well as theoretical significance. The relative importance of requirements

TABLE 14.1. Approximate Proportions of the Total Energy Requirements of Animals which are contributed by their Requirements for Maintenance

	Required for:		Maintenance as a percentage of total
	Maintenance	Production	
<i>Daily values (kcal net energy)</i>			
Dairy cow weighing 1100 lb and producing 40 lb milk	8000	13,600	37
Steer weighing 700 lb and gain- ing 2 lb	7000	3200	69
Pig weighing 100 lb. and gaining 1.5 lb	1200	3000	29
Fowl weighing 1000 g and gaining 27 g	120	60	66
<i>Annual values (Mcal net energy)</i>			
Dairy cow weighing 1100 lb, pro- ducing a calf of 80 lb and 9000 lb milk	2920	3060	49
Sow weighing 450 lb, producing 16 piglets, each 3.5 lb at birth, and 2000 lb milk	1100	1160	49
Hen weighing 2000 g, producing 220 eggs	45	20	69

* Technical reviews and summaries of the nutrient requirements of ruminants were published in December 1965; see reference 19 in the Appendix, p. 390.

for maintenance is illustrated in Table 14.1, which shows the proportion of their total energy requirements used for this purpose by various classes of animal.

Animals deprived of food are forced to draw upon their body reserves to meet their nutrient requirements for maintenance. We have seen already that a fasted animal must oxidise reserves of nutrients to provide the energy needed for such essential processes as respiration and the circulation of the blood. Since the energy so utilised leaves the body, as heat, the animal is then in a state of negative energy balance. The same holds true for other nutrients: an animal fed on a protein-free diet continues to lose nitrogen in its faeces and urine, and is therefore in negative nitrogen balance. The purpose of a maintenance ration is to prevent this drain on the body tissues, and the maintenance requirement of a nutrient can therefore be defined as the quantity which must be supplied in the diet so that the animal experiences neither net gain nor net loss of that nutrient. The requirement for maintenance is thus the minimum quantity promoting zero balance. (The qualification 'minimum' is necessary, because if the animal is unable to store the nutrient in question, increasing the quantity supplied above that required for maintenance will still result in zero balance.)

Energy Requirements for Maintenance

Basal and fasting metabolism. It was explained earlier (p. 156) that energy expended for the maintenance of an animal is converted into heat and leaves the body in this form. The quantity of heat arising in this way is known as the animal's *basal metabolism*, and its measurement provides a direct estimate of the quantity of net energy which the animal must obtain from its food in order to meet the demand for maintenance. The measurement of basal metabolism is complicated by the fact that the heat produced by the animal does not come only from this source, but comes also from the digestion and metabolism of food constituents (the heat increment of feeding), and from the voluntary muscular activity of the animal. Heat production may be further increased if the animal is kept in a cold environment (see p. 223).

When basal metabolism is measured, the complicating effect of the heat increment of feeding is removed by depriving the animal of food. The period of fast required for the digestion and metabolism of previous meals to be completed varies considerably with species. In Man an overnight fast is sufficient, but in ruminant animals digestion, absorption and metabolism continue for several days after feeding ceases, and a

fast of at least four days would be needed. The same period is recommended for the pig, and two days for the fowl. There are a number of criteria for establishing whether the animal has reached the post-absorptive state. If heat production can be measured continuously, the most satisfactory indication is the decline in heat production to a steady, constant level. A second indication is given by the respiratory quotient (p 166). In fasting, the oxidation mixture gradually changes from absorbed fat, carbohydrate and protein to body fat and some body protein. This replacement in the mixture of carbohydrate by fat is accompanied by a decline in the non protein respiratory quotient, and when the theoretical value for fat (0.7) is reached it may be assumed that energy is being obtained only from body reserves. In ruminants an additional indication that the postabsorptive state has been reached is a decline in methane production (and therefore digestive activity) to a very low level.

The contribution of voluntary muscular activity to heat production can be reduced to a low level when basal metabolism is measured in human subjects, but in farm animals the cooperation needed to obtain a state of complete relaxation can rarely be achieved. Fasting may limit activity, but even the small activity represented by standing as opposed to lying is sufficient to increase heat production by about 12 per cent. Consequently the term *fasting metabolism* is to be preferred to basal metabolism in studies with farm animals, since strict basal conditions are unlikely to be observed.

A term used in conjunction with fasting metabolism is *fasting katabolism*. This includes the relatively small quantities of energy lost by fasting animals in their urine.

Some typical values for fasting metabolism are given in Table 14.2. As one would expect, the values are greater for large than for small animals, but column 2 shows that per unit of liveweight, fasting metabolism is greater in small animals. At an early stage in the study of basal metabolism it was recognised that fasting heat production is more nearly proportional to the surface area of animals than to their weight, and it became customary to compare values for animals of different sizes by expressing them in relation to surface area (column 3 of Table 14.2). The surface area of animals is obviously difficult to measure, and methods were therefore devised for predicting it from their body weight. The basis for such methods is that, in bodies of the same shape and of equal density, surface area is proportional to the two thirds power of weight (*W^{2/3}*). The logical development of this approach was to omit the calculation of surface area and to express

fasting metabolism in relation to $W^{0.67}$ When the relation between fasting metabolism and body weight was examined further, however, it was found that the closest relationship was between metabolism and $W^{0.73}$, not $W^{0.67}$ The former function (or the nearly similar $W^{0.75}$) has therefore come into use as a reference base for fasting metabolism (column 4 of Table 14.2)

TABLE 14.2 Some typical Values for the Fasting Metabolism of Adult Animals of various Species

Animal	Live-weight (kg)	Fasting metabolism (kcal/day)			
		Per animal (1)	Per kg liveweight (W) (2)	Per sq metre surface area (3)	Per $W^{0.73}$ (4)
Cow	500	7470	14.9	1530	80
Pig	72	1342	18.6	920	59
Man	70	1700	24.3	950	77
Sheep	50	1060	21.2	890	61
Fowl	3.5	187	53.4	—	75
Rat	0.29	28.1	96.9	840	69

There has been considerable discussion whether surface area or $W^{0.73}$ (often called *metabolic liveweight*) is the better base. This will not be repeated here, but is contained in the books listed at the end of the chapter. Mathematically there is nothing to choose between the two bases, for their relationships with fasting metabolism are equally close.

The fasting metabolism of adult animals of species ranging in size from mice to elephants has an average value of 70 kcal per kg $W^{0.73}$ per day, but there are considerable variations from species to species. Among farm animals, cattle have a fasting metabolism about 15 per cent higher than the inter-species mean, and sheep a fasting metabolism 15 per cent lower. There are also variations within species, notably those caused by age and sex. Fasting metabolism per unit of metabolic liveweight is higher in young animals than in old, being for example 120 kcal per kg $W^{0.73}$ in a young calf but only 80 kcal per kg $W^{0.73}$ in a mature cow. It also tends to be higher in males than in females.

Estimating maintenance energy requirements from measurements other than those of fasting metabolism. The quantity of energy required for maintenance is, by definition, that which promotes energy equilibrium (zero energy balance). This quantity can be estimated directly in fed, as opposed to fasting, animals if the energy content of their food is known and their energy balance can be measured. The maintenance

requirements of cattle were estimated in this manner by Kellner in experiments in which rations of known starch equivalent were given. In theory the quantities of food given could have been adjusted until the animals were in exact energy equilibrium, but in practice it was found easier to allow them to make gains, and then to calculate the starch equivalent required to promote these gains. For example, in one experiment five oxen with an average weight of 1520 lb were given rations providing 9.75 lb starch equivalent per day, and retained an average of 0.92 lb fat or 3950 kcal per day. The starch equivalent needed to promote this energy retention was calculated to be $3950/1071 = 3.69$ lb (since 1 lb starch promotes a storage of 1071 kcal), and so $9.75 - 3.69 = 6.06$ lb starch equivalent was required for maintenance.

Kellner's approach can also be followed in feeding trials in which animals are not kept in calorimeters. The animals are given known quantities of food energy, and their liveweights and liveweight gains or losses are measured. The partition of energy intake between that used for maintenance and that used for liveweight gain can be made in two ways. The more simple method involves the use of known feeding standards for liveweight gain. The alternative is to analyse the figures for energy intake (I), liveweight (W) and liveweight gain (G) by solving equations of the form

$$I = aW^{0.75} + bG$$

The coefficients a and b then provide estimates of the quantities of food energy used for maintenance and for each unit of liveweight gain respectively. This form of analysis can be extended to animals with more than one type of production, such as dairy cows, by adding extra terms to the right hand side of the equation.

The main objection to determining energy requirements for maintenance (and also for production) in this way is that liveweight changes may fail to give a correct measure of energy balance. It is possible, however, to put the method on a sounder 'energy' basis by using the comparative slaughter technique to estimate changes in the energy content of the animals. The 'feeding trial' method has the considerable advantage of estimating the maintenance requirements of animals when they are kept under normal farm conditions, rather than under the somewhat unnatural conditions represented by a fast in a calorimeter. As discussed below, it is often difficult to translate values for fasting metabolism into practical maintenance requirements.

The activity of the animal and its maintenance requirement In animals kept under normal farm conditions the quantities of energy required to maintain energy equilibrium may well be greater than in animals kept

in a calorimeter. In the first place, animals on the farm commonly use more energy for voluntary muscular activity. Secondly, farm animals experience greater extremes of climate and may need to use energy specifically to maintain their normal body temperature. The effects of climate on energy requirements for maintenance are discussed later in this chapter.

Energy used for voluntary muscular activity is regarded as part of the maintenance requirement, and must be taken into account when values for fasting metabolism are translated into allowances for maintenance. The maintenance requirement of an animal on the farm is therefore composed of its fasting metabolism and an addition, known as the *activity increment*, for the extent to which its activity is greater than it would be in a calorimeter. The activity increment can be estimating directly, for example by measuring in a calorimeter the energy needed for walking on a treadmill, or indirectly, by comparing the fasting metabolism with estimates of maintenance requirement obtained in feeding trials when the animal is in its normal environment.

The activity of an animal housed under farm conditions is likely to differ from that of an animal in a calorimeter more in degree than in kind. In particular, the farm animal may spend more of its time in a standing position. The extra energy needed for standing rather than lying has been investigated in calorimetric trials, but the results obtained have varied remarkably. For ruminant animals, however, the results suggest that heat production during standing is of the order of only 12 per cent. greater than during lying, and since the time spent standing by the farm animal is unlikely to exceed that for the calorimeter animal by more than 6 hours, the activity increment of housed ruminants is presumed to be small. This conclusion is not very well supported by estimates of activity increment obtained by comparing fasting metabolism with feeding-trial determinations of maintenance requirements. Estimates obtained in this way range from 0 to 50 per cent. of the fasting metabolism. For non-ruminants kept indoors the activity increment is considered to be as much as 50 per cent. of the fasting metabolism.

In grazing animals the maintenance requirement will be increased by the energy costs of locomotion and of the muscular activity involved in harvesting pasture herbage. The energy cost of walking on the level is known to be a relatively small item in this account. Sheep, for example, require 0.6 kcal per kg body weight per km travelled, and so a 50 kg lowland sheep, walking perhaps 2 km per day, would require 60 kcal for this purpose (or about 6 per cent. of its fasting metabolism). Few estimates have been made of the energy expended by a grazing

animal in harvesting its food, but it appears that the activity involved might be sufficient to increase the maintenance requirement by as much as 20 per cent. of the fasting metabolism. A summation of the energy costs of its various activities suggests that the activity increment of a grazing animal will be 25-50 per cent of its fasting metabolism. This 'theoretical' range is again lower than 'practical' estimates obtained via analyses of the feed intakes and production of grazing animals. Practical estimates have ranged from 25 to 100 per cent of the fasting metabolism and have mostly been greater than 50 per cent.

It must be concluded that activity increments can be estimated only imperfectly, and that the translation of values for fasting metabolism, however accurately measured, into maintenance energy requirements must be somewhat inaccurate. The errors involved in basing requirements on fasting metabolism data will, however, be small for animals kept under conditions of close confinement. For more active animals it may well be that 'practical' estimates of maintenance energy, obtained by analysis of food intake and of the animal production resulting from it, will be more meaningful than standards derived from the fasting metabolism, but it is doubtful whether such practical estimates can yet be obtained accurately enough to justify their use as feeding standards.

Present standards For cattle, the standard which has been used in the United Kingdom for many years (Appendix Tables 7 and 8) has been that recommended by Kellner. According to this an animal weighing 1000 lb should be given 6.0 lb starch equivalent per day for maintenance, from which allowances for animals of other weights are calculated on the basis of surface area. The allowance for an animal of 750 lb is therefore $6.0 \times (750/1000)^{0.75} = 4.9$ lb starch equivalent. If 1 lb starch equivalent supplies 1400 kcal net energy for maintenance, 6 lb supplies 8400 kcal. Kellner did not measure fasting metabolism, but since his time the fasting metabolism of cattle of 1000 lb liveweight has been found to average about 8300 kcal per day at two years of age and 7000 kcal per day at and above four years. These figures are in reasonable agreement with Kellner's standard (which includes a safety factor), and therefore any new standard which is based on the fasting metabolism is unlikely to differ much from Kellner's, as far as housed animals are concerned. For grazing cattle, Wood in *Rations for Livestock* proposed that Kellner's standard should be increased by from 1 lb starch equivalent for good quality grazing to 3 lb for poor quality. While these additions are arbitrary, and perhaps too low, no better ones can be suggested at the present time.

For sheep, the standards originally used in this country were calculated by Wood from the estimated starch equivalent intakes of housed sheep and their liveweights and liveweight changes. There is now evidence, both from further 'practical' estimates of requirements and from determinations of fasting metabolism, that Wood's standards are too high for housed sheep, and lower values are given in Appendix Table 9.

The energy requirements of growing pigs and poultry are normally stated for maintenance *plus* growth combined, and there are no standards for maintenance alone. Laying hens are normally fed to appetite, although a standard for maintenance energy for them has been suggested by the Agricultural Research Council's Technical Committee on the Nutrient Requirements of Farm Livestock. This standard is based on analyses of energy intake, animal liveweight and production, and rises from 185 kcal metabolisable energy per day for birds of 1500 g to 370 kcal for birds of 3000 g. (This implies that the requirement varies directly with liveweight.)

The Influence of Climate on Requirements of Energy for Maintenance

Mammals and birds are *homeotherms*, which means that they attempt to keep their body temperature constant. Animals produce heat continuously and, if they are to maintain a constant body temperature, must lose it to their surroundings. The routes by which they may lose heat are by radiation, conduction and convection from their body surface, and by the evaporation of water from both their body surface and their lungs. The rate at which heat is lost depends in the first instance on the difference in temperature between the animal and its surroundings; for farm animals the rectal temperature, which is slightly lower than the deep body temperature, lies in the range 36–43° C. The rate of heat loss is influenced also by characteristics of the animal, such as the insulation provided by its tissues and coat, and by such characteristics of the environment as air velocity, relative humidity and solar radiation. In effect, the rate of heat loss is determined by a complex interaction of factors contributed by the animal and its environment, but it is only the effect of air temperature which has been reasonably well investigated. For housed animals, of course, air temperature is the most significant feature of the environment.

The animal must achieve homeothermy in the face of potential variations in both heat production and rate of heat loss, and it has only partial control over these variations. In general an animal will adjust to changes in its environment first by altering its rate of heat loss; only

if these measures are insufficient will it alter its heat production. Let us consider the case of a pig kept under basal conditions, i.e. fasting, resting and at a 'comfortable' air temperature of 25°C (Fig 14 1, line A). If the air temperature is then gradually reduced, the pig maintains its body temperature by reducing its rate of heat loss, principally by reducing the circulation of blood to the skin. As the fall in air temperature continues, however, a stage is reached when the pig

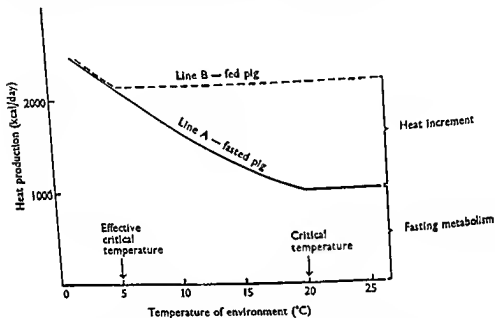


FIG 14 1 Effect of environmental temperature on the heat production of the pig

can maintain its body temperature only by increasing its heat production. This increase might be achieved through the muscular activity of shivering. The temperature below which heat production is increased is known as the *critical temperature*. In Fig 14 1 this is 20°C. Heat produced specifically to maintain body temperature represents an extra drain on the fasting animal's energy reserves and must be regarded as a part of the requirement of energy for maintenance. Thus we should expect that at temperatures below 20°C a pig would need a higher energy intake to promote energy equilibrium than it would at higher temperatures. In a pig given food (Fig 14 1, line B), however, the situation is rather different. At the 'comfortable' temperature of 25°C, heat production is greater in the fed than in the fasting pig because of the heat increment of the food. This means that the air temperature can fall to considerably below 20°C before the fed pig needs to shiver.

and produce more heat. This lower temperature, 5°C in the example, is sometimes known as the *effective critical temperature*. While it is obviously of greater practical significance than the critical temperature recorded for the fasting animal, even the effective critical temperature has limitations as a guide to whether or not animals are likely to have their energy requirements increased by their environment. The effective critical temperature will vary with the quantity of food consumed and with the efficiency with which it is metabolised. In the pig it will also vary from time to time during the day, for the contribution to total heat production of the heat increment of the food will be greater shortly after a meal than immediately before it. (In ruminants there will be less diurnal variation because absorption and metabolism are more continuous than in simple-stomached animals)

When one turns to consider the effect of the environment on the energy transactions of animals kept out of doors, where there are more variables, the situation becomes decidedly more complex. The complexities are well illustrated by the experiments of K. L. Blaxter, who has recently shown that the effective critical temperature of Cheviot sheep fed at a maintenance level of nutrition varies between -3 and 24°C according to the length of their fleece (10–100 mm) and the wind speed to which they are exposed (0–15 mile/h). For sheep with a 55-mm fleece, the effective critical temperature was estimated to increase from 1°C when there was no air movement to 16°C at a wind speed of 15 mile/h. In sheep kept on the uplands of Britain there is little doubt that the requirement of energy for maintenance is frequently increased by the environment, but it is difficult to assess the size of the increase.

In a cold environment the animal's problem is one of conserving heat, but in a hot one the problem becomes that of disposing of the heat produced. As air temperatures increase, less heat is lost by radiation, conduction and convection and more has to be dissipated through the evaporation of water. Farm animals are less efficient than Man in losing heat by evaporation from the skin surface, and must often make the maximum use of the other route of evaporative loss, through the lungs. Panting increases respiratory evaporative losses, but it also increases heat production and hence the maintenance requirement of the animal. If all efforts to keep body temperature constant fail, the rise in body temperature which results will itself increase heat losses by radiation, conduction and convection. This is no safety valve, however, since a rise in body temperature causes the rate of metabolism, and hence of heat production, to increase.

Protein Requirements for Maintenance

An animal placed on a nitrogen free, but otherwise adequate, ration continues to lose nitrogen in its faeces and urine. The nitrogen of the faeces, as described earlier (Chapter 10), arises from the enzyme and cell residues of the digestive tract. If the animal continues to eat, it must continue to lose nitrogen in this fashion.

It is less obvious, perhaps, why an animal on a nitrogen free diet should lose nitrogen in its urine. In part this excretion represents nitrogen which has been incorporated into materials subsequently expended, and which cannot be recovered by the body for re use. Thus the creatine of muscles is eventually converted into creatinine, which is excreted in the urine. But the greater part of the nitrogen in the urine of animals not receiving food nitrogen is (in mammals) in the form of urea, the typical by product of amino acid catabolism. The significance of this urea nitrogen was not fully appreciated until experiments with isotopically labelled amino acids had shown that the proteins of body tissues are not static but are constantly being broken down and replaced. The turnover rate of body proteins varies considerably from one tissue to another, proteins are replaced at intervals of hours or days in the intestine and liver, whereas in bone and nerve the interval may be one of months or even years. The amino acids released when body proteins are broken down form a pool from which the replacement proteins are synthesised, a particular amino acid molecule may therefore be present one day in a protein of the liver, for example, and the next day in muscle protein. In effect the body proteins exchange amino acids among themselves. Like the synthesis of body proteins from absorbed amino acids (Chapter 13), however, this domestic traffic in amino acids is not completely efficient. Acids liberated from one protein may fail to be incorporated in another and are katabolised, their amino groups thus yielding the urea which is excreted in the urine.

When an animal is first placed on a nitrogen free diet, the quantity of nitrogen in its urine may fall progressively for several days before stabilising at a lower level and when nitrogen is re introduced into the diet there is a similar lag in the re establishment of equilibrium. This suggests that the animal possesses a protein reserve which can be drawn upon in times of scarcity of dietary nitrogen and restored in times of plenty. In times of scarcity, the tissues most readily depleted of protein are those in which the proteins are most labile, such as the liver. Depletion of liver nitrogen is accompanied by some reduction in enzyme activity, and the 'reserve protein' is therefore envisaged as a

'working reserve' which consists of the cytoplasmic proteins themselves

Once the reserve protein has been depleted, the urinary nitrogen excretion of an animal deprived of food nitrogen reaches a minimal and approximately constant level (This level will be maintained only if energy intake is adequate, for if tissue proteins are katabolised specifically to provide energy, urinary nitrogen excretion will rise again) The nitrogen excreted at this minimal level is known as the *endogenous urinary nitrogen*, and represents the smallest loss of body nitrogen commensurate with the continuing existence of the animal. The endogenous urinary nitrogen excretion can therefore be used to estimate the nitrogen (or protein) required by the animal for maintenance. It is analogous to the basal metabolism, and in fact there is a relationship between the two. The proportionality commonly quoted is 2 mg endogenous urinary nitrogen per kcal basal metabolism. Endogenous urinary nitrogen excretion, like basal metabolism, is considered to vary not with liveweight itself but with metabolic liveweight ($W^{0.75}$).

When nitrogen is re-introduced into the diet, the quantity of nitrogen excreted in the urine increases through the wastage of amino acids incurred in utilising the food protein. Urinary nitrogen in excess of the endogenous portion is known as the *exogenous urinary nitrogen*. This name implies that such nitrogen is of food origin as opposed to body origin, but, with the exception of the creatinine fraction of the endogenous portion, it is doubtful whether such a strict division of urinary nitrogen is justified. It is more realistic to regard the so called exogenous fraction as the extension of an existing loss of nitrogen rather than as an additional source of loss, for it probably reflects simply an increase in turnover and wastage of amino acids.

The quantity of nitrogen or of protein required for maintenance is that which will balance the metabolic faecal and endogenous urinary losses of nitrogen (and also the small dermal losses of nitrogen occurring in scurf, hair and sweat). The two most commonly employed methods for estimating this quantity are analogous to those used for determining the quantity of energy needed for maintenance. The first, analogous to the determination of the fasting katabolism, involves measuring the animal's losses of nitrogen when it is fed on a nitrogen free diet, and calculating the quantity of food nitrogen required to balance these losses. In the second method, the quantity of food nitrogen required is determined directly by finding the minimum intake which produces nitrogen equilibrium. This method is similar to that used by Kellner for estimating maintenance energy requirements (p. 219).

Estimating protein requirements for maintenance from endogenous urinary and metabolic faecal nitrogen (the factorial method) Like the measurement of fasting katabolism, the measurement of endogenous urinary and metabolic faecal nitrogen presents considerable practical difficulties. Animals show a disinclination to eat nitrogen free diets, and in ruminants the microbial digestion of the constituents of such diets is often impaired. In addition considerable time may be needed for urinary nitrogen to reach a minimal and constant level.

Once they are obtained, values for nitrogen excretion can be translated into requirements for dietary protein in the following manner. Suppose that the animal to be considered is a cow of 1000 lb liveweight, and that its output of metabolic faecal nitrogen, which varies with dry matter intake (see Chapter 10), has been found to be 0.5 lb N per 100 lb food dry matter. Suppose also that endogenous urinary nitrogen amounts to 0.023 lb per day. If the cow ate 25 lb dry matter per day, the net requirement for protein would be

$$6.25 (25/100 \times 0.5 + 0.023) = 0.92 \text{ lb/day}$$

To convert this figure into digestible protein we have to take into account that absorbed protein is not utilised with 100 per cent efficiency. The efficiency of utilisation is expressed in the biological value of the protein, which for ruminants is frequently assumed not to vary much from 70 per cent. The above net requirement for protein is therefore converted into digestible crude protein by multiplying it by 100/70

$$0.92 \times 100/70 = 1.31 \text{ lb/day}$$

Now, as metabolic faecal nitrogen has already been taken into account, the requirement of 1.31 lb is for *truly* digestible protein. Most values given in tables of food composition are for *apparently* digestible protein, and we therefore convert the requirement into apparently digestible protein by deducting the metabolic faecal protein

$$1.31 - 6.25 (25/100 \times 0.5) = 0.53 \text{ lb/day}$$

The steps by which this requirement for digestible crude protein is obtained are summarised in the equation

$$R = 6.25 \{100/B (M \times D + E) - M \times D\},$$

where R = requirement of digestible crude protein (lb/day),

B = biological value of food protein (per cent),

M = metabolic faecal nitrogen (lb/100 lb food dry matter intake),

D = dry matter intake (100 lb/day),

E = endogenous urinary nitrogen (lb/day)

The reason for including metabolic faecal nitrogen in the first stage of the calculation and then subtracting it when converting truly to apparently digestible protein, is to allow for the wastage of amino acids incurred in the synthesis of metabolic faecal protein. Thus it is assumed that, for each 1 g of metabolic faecal protein excreted, the animal must absorb and metabolise $1 \times 100/70 = 1.43$ g.

Metabolic faecal protein is an important item in determining the protein requirement of the ruminant. It should be noted that if the requirement is stated in terms of digestible protein it will vary with food intake. If the cow in the example above were fed on a more concentrated diet, and ingested 20 and not 25 lb dry matter per day, its requirement would be only 0.48 lb digestible crude protein per day instead of 0.53 lb. In order to avoid this complicating effect of food intake, protein requirements are sometimes expressed as *available protein*. The requirement of available protein for maintenance is calculated by omitting metabolic faecal nitrogen entirely from the general equation given immediately above. This leaves

$$6.25 \times 100/B \times E$$

If feeding standards are expressed as available protein, then the protein values of foods should be stated in the same terms. The available protein content (per cent of dry matter) of a food is its digestible crude protein content less that protein wasted in the synthesis of metabolic

faecal protein, i.e. less $6.25 \left(M \times \frac{100-B}{B} \right)$. Alternatively, standards may be expressed initially as available protein and then translated into digestible crude protein for specific rationing situations where food intake, and hence metabolic faecal nitrogen excretion, is known.

As will be shown later, this factorial method for estimating protein requirements can also be used to determine the requirements of productive animals. The method is based on sound principles, but has sometimes yielded values that differ from those obtained by other methods, being generally lower. Such disagreement may be due to the difficulties of determining the basic data used in factorial calculations. It is likely also that endogenous urinary and metabolic faecal nitrogen are not the 'constants' they are often considered to be.

Estimating protein requirements from nitrogen balance trials If animals are fed on a number of rations which supply equal amounts of dry matter and energy, but varying amounts of protein, their nitrogen balances can be expected to form a curve of the type shown in Fig. 14.2

As nitrogen intake increases from a low level, there is a gradual reduction in the negative balance until the point of equilibrium is reached. The extent to which further increments of food nitrogen promote nitrogen storage will depend on the age of the animals and the supply of other nutrients. A stage is eventually reached, however, when further increments of protein fail to promote further nitrogen retention, and the curve then becomes horizontal. Mature animals may store

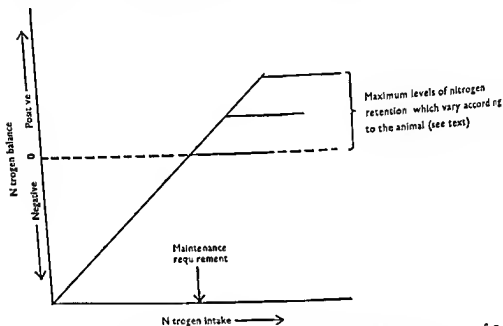


FIG 14.2 Stylised representation of the assessment of protein requirements for maintenance by means of nitrogen balance trials

very little nitrogen, in which case the curve will become horizontal at a nitrogen balance close to zero (the lowest horizontal line in Fig 14.2)

When maintenance protein requirements are determined in nitrogen balance trials, sufficient negative and positive balances are obtained by using rations supplying different quantities of protein, to enable lines like those of Fig 14.2 to be constructed. Care is needed in interpreting positive balances, since these may be represented by points on the horizontal part of the curve. A further difficulty to be borne in mind is that the protein intake required to promote equilibrium will depend to some extent on the previous nutrition of the animals. If the animals are well supplied with reserve protein, a higher intake will be needed to maintain equilibrium than if their reserves are depleted.

Present standards. Although sufficient information exists on metabolic faecal and endogenous urinary nitrogen losses for maintenance requirements to be calculated for most classes of animal, standards for maintenance protein are used only in the feeding of dairy cows. For other classes of stock, protein standards are expressed for maintenance and growth combined, and a discussion of them is delayed until later in this chapter. For dairy cows the standard used in the United Kingdom for many years was 0.65 lb digestible crude protein per day for a cow of 1000 lb liveweight. This is higher than the standards used in other countries, and the value now advocated is 0.6 lb digestible crude protein per day for a 1000-lb animal.

FEEDING STANDARDS FOR GROWTH, FATTENING AND WOOL PRODUCTION

Growth in farm animals is most commonly measured in terms of increase in liveweight.* The typical pattern of liveweight growth is as

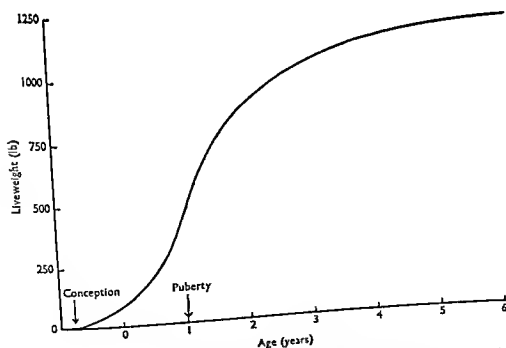
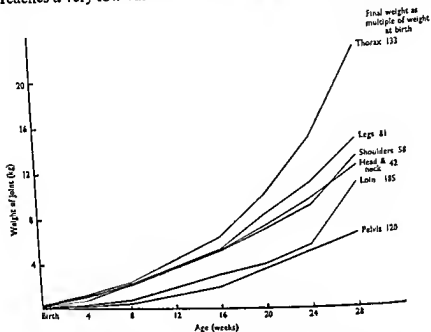


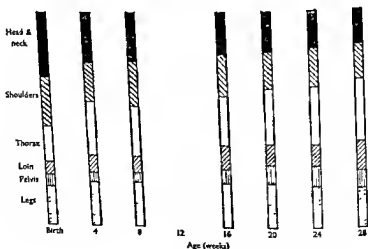
FIG 14.3. The typical sigmoid growth curve as it would appear for the dairy cow.

* Liveweight increase consists of growth of the animal's tissues together with additions to the contents of its gut. In non-ruminants the proportion of liveweight increase which consists of gut contents will be small, but in ruminants it may be as high as 12 per cent.

shown in Fig. 14.3. During the foetal period and from birth to about puberty the rate of growth accelerates; after puberty it decelerates and reaches a very low value as the mature weight is approached.

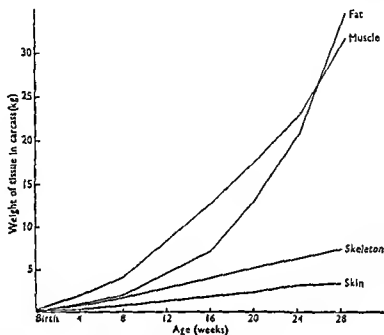


(a) Growth rates of various parts of the body.

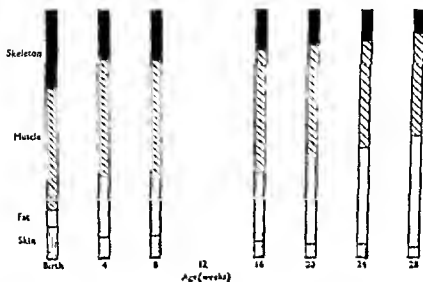


(b) Relative proportions of the dressed carcass at various stages.

Animals which are growing do not simply increase in size and weight—they also show development. By this we mean that the various parts of the body grow at different rates, so that its proportions change as the animal matures. Such developmental changes can be demonstrated



(a) Growth rates of the tissues.



(b) Composition of the carcass at various ages.

FIG. 14.5. Age changes in the composition of the pig carcass. (After C. P. McMeekan, 1940. *J. agric. Sci.* 30, 276.)

by slaughtering animals at different ages and weights and dissecting them into their various joints. Fig 14 4, which was derived in this way, shows that in bacon pigs the thorax, loin and pelvis grow relatively faster than the head, neck and shoulders, which thus form a progressively smaller proportion of the carcass as the animal increases in size.

Developmental changes also occur in the relative proportions of the major body tissues. The pig carcasses considered in Fig 14 4 were dissected into their various tissues, with the results shown in Fig 14 5. In the young pig growth is largely in terms of muscle, but as the animal

TABLE 14 3 Body Composition of Lambs Slaughtered at 5 and 10 Months of Age, and the calculated Composition of the Liveweight Gains of Lambs between these Ages (Based on data given by H. H. Mitchell, W. G. Kammlade and T. S. Hamilton, 1928 *Bull. Ill agric. Exp. Stn.*, No. 314)

	Live weight (lb)	Weight (lb) of					Energy content of body (Mcal)
		Water	Crude protein	Ether extract	Ash	Calcium	
Composition of lambs slaughtered at about 5 months old	58.5	39.14	9.59	6.96	2.35	0.67	52.35
Composition of lambs slaughtered at about 10 months old	86.7	48.86	13.43	19.16	3.22	0.72	112.10
Composition of gains	28.2	9.72	3.84	12.20	0.87	0.05	59.75
Percentage composition of gains	—	36.5	14.4	45.8	3.27	0.19	2244*

* kcal/lb

matures there is a remarkable increase in the fat content of the carcass. These changes in tissue proportions with age are accompanied, as one would expect, by changes in the chemical composition of the animal body. As an animal increases in weight its proportions of protein, ash and water decrease and its proportion of fat increases. It follows that the composition of gains made by animals will change as they grow, and therefore that the nutrients required for each unit of gain will differ in quantity according to the degree of development of the animal.

The composition of liveweight gains. The composition of the gains made by animals during various stages of growth can be determined by the comparative slaughter technique described in Chapter 11, and an example of such a determination is given in Table 14 3. In the experiment from which this example is drawn, a group of lambs were killed at an average liveweight of 58.5 lb, and their bodies analysed.

A comparable group were fed until their average liveweight reached 86.7 lb, and were then killed and analysed in the same manner. The quantities of protein, ether extract etc. stored by the second group while growing from 58.5 to 86.7 lb have been calculated by assuming that at the lower weight these lambs had been similar in composition to those slaughtered in the first group.

The composition of gains made by several species is shown in Table 14.4. As an animal ages the general tendency is for there to be a progressive decline in the water content of its gains, a slight fall in protein

TABLE 14.4. Percentage Composition and Energy Content of the Gains made by Animals at various Ages and Liveweights

Taken from H. H. Mitchell, 1962, *Comparative Nutrition of Man and Domestic Animals*, Vol. 1 (Academic Press, New York and London)

Animal	Live-weight (lb)	Age	Composition of gain				
			Water (per cent)	Protein (per cent)	Fat (per cent)	Ash (per cent)	Energy (kcal/lb)
Cow (White Leghorn pullets—slow growth)	0.5	4.4 weeks	69.5	22.2	5.6	3.9	1.49
	1.5	11.5 "	61.9	23.3	8.6	3.7	2.39
	3.0	22.4 "	56.5	14.4	25.1	2.2	3.07
Sheep (Shropshire ewes)	19	6.0 months	57.9	15.3	24.8	2.2	3.32
	75	11.3 "	48.0	16.3	32.4	3.1	3.94
	131	24.7 "	25.1	15.8	52.8	6.3	4.97
Pig (Duroc-Jersey females)	50	—	39	12.7	46	2.9	5.03
	100	—	38	12.4	47	2.8	5.11
	250	—	34	11.0	52	2.4	5.58
Cow (Holstein heifers)	150	1.3 months	67.1	19.0	8.4	—	1.87
	500	10.6 "	59.4	16.5	18.9	—	2.72
	1000	32.4 "	55.2	20.9	18.7	—	2.95

content and a marked rise in fat content. These changes lead to a rise in the energy content of each unit of gain. The term 'fattening' is used in agricultural practice to describe the later stages of growth, but it is misleading to think of muscle and bone growth occurring as a separate and earlier phase. The gains of young animals almost invariably contain some fat, and those made by older animals only come to consist entirely of fat when an advanced stage of maturity has been reached. (Of the energy retained by Kellner's 1500-lb steers, for example, about 10 per cent. was in the form of protein.) All meat animals are considered to have reached a marketable size long before their gains come to consist of fat alone.

Most information on the composition of liveweight gains has been obtained with animals growing at what are considered today to be rather slow rates. There is very little information on, for example, the composition of gains made by cattle with a liveweight increase of more than 2 lb per day, or by chicks growing from birth to slaughter at an average rate of 30 g per day. From rather limited evidence it appears that at a given liveweight the gains of faster-growing animals contain a higher proportion of fat and lower contents of protein and water than those of animals growing more slowly.

There is a shortage of information also on the composition of gains made by individuals whose growth curves have departed widely from the curves characteristic of their species. If an animal is unusually heavy for its age, for example, will the composition of its gains be characteristic of an average (and older) animal of the same weight or of one of the same age? From limited evidence again, the tentative conclusion is that the composition of gains is determined more by the weight of the animal and its degree of development than by its age.

Energy Requirements for Growth

Ruminants The most comprehensive investigation of the composition of gains in cattle was the Missouri 'Use of feed' experiment, in which animals were reared at three rates of growth (approximately $\frac{1}{4}$ lb, 1 lb and $\frac{3}{4}$ lb liveweight gain per day) and slaughtered at ages between 1 month and 4 years.

The results of this investigation have been re-analysed on several occasions, and some figures from the latest analysis are given in Table 14.5. These show, first, that the energy retained per unit of gain increases as the animal matures, and second, that at a given age a fast-growing animal retains more energy per unit of gain than a slow growing one (although this difference is less if the comparison is made at a given weight rather than a given age). Feeding standards for growth in cattle are based on the results of the Missouri investigation and of others like it, but they have also been influenced by the results of other feeding trials in which only liveweight gains were measured.

Standards based on those which have been used in the United Kingdom for many years are shown in Appendix Table 8. The columns of this table headed 'Slow growth' are appropriate for beef cattle growing relatively slowly for two years and then being fattened rapidly, and they are applicable also to the rearing of dairy heifers. Other columns give tentative standards for faster growing animals gaining an average of about 2 lb per day. If these standards are compared with the results

of comparative slaughter experiments, by assuming that an allowance of 1 lb starch equivalent promotes the retention of 1071 kcal, the standards appear rather generous. For example, an animal of 600 lb gaining 1 lb per day is considered to require 1.85 lb starch equivalent per lb of gain, which implies a retention of $1071 \times 1.85 = 1981$ kcal per lb of gain. In the Missouri experiment, however, similar animals were calculated to be storing only about 1540 kcal per lb of empty body gain or approximately 1350 kcal per lb of liveweight gain. (The

TABLE 14.5 The Energy Content of Gains in Empty Body Weight * made by Cattle growing at Different Rates (kcal/lb)
(Calculated from the data of C. R. Moulton, P. F. Trowbridge and L. D. Haigh, *Res. Bull. Mo. agric. Exp. Sta.*, No. 55, 1922, by K. L. Blaxter in *The Energy Metabolism of Ruminants*, 1962, p. 169. Hutchinson, London)

Age of animal (months)	Growth rate		
	Fast (c. $1\frac{1}{2}$ lb/day)	Medium (c. 1 lb/day)	Slow (c. $\frac{1}{2}$ lb/day)
3	1360	1090	860
6	1500	1180	910
9	1680	1320	1000
12	1860	1500	1040
18	2270	1630	1320
24	2680	1900	1450

* The energy content of gains in liveweight would be about 15 per cent less than the values shown in this table.

latter figure is lower because liveweight gain includes gut contents.) For sheep the information available on the caloric content of liveweight gains is more limited even than that for cattle. Appendix Table 9, part 2, gives the standards from *Rations for Livestock*, which are based mainly on data from feeding trials.

Pigs. Feeding standards for pigs, unlike those for ruminants, do not normally include values for the dietary energy needed for each unit of growth at different ages or weights. The reason is not that the basic information on the energy content of gains is lacking, but rather that pigs are not rationed to induce a particular liveweight gain per day, as ruminants frequently are. The basic aim in rationing pigs is to encourage the fastest possible rate of growth that can be obtained without excessive deposition of fat. The fastest growth is achieved by allowing the pigs to eat to appetite, and some types of pig can eat to appetite from birth until slaughter at 'bacon weight' (200 lb) without laying down too much fat. With most pigs, however, food

intake must be restricted during growth from when they reach 100 lb, or even 50 lb, if a sufficiently lean carcass is to be obtained. Feeding scales have therefore been devised which stipulate the quantities of food to be given at different liveweights. A typical scale would allow the pigs to eat to appetite until they reached 100 lb in liveweight and were eating 5 lb of meal per day, thereafter the allowance would be restricted to about 80 per cent of appetite, reaching $6\frac{1}{2}$ lb of meal at 200 lb liveweight. Such restriction of intake slows down the rate of growth, but it reduces the fat content of the carcass and makes the carcass more acceptable to the bacon curer.

When feeding scales are used, it is restriction of energy intake rather than restriction of protein or other nutrients that limits growth, and therefore the scales are, in a sense, energy standards for growth and maintenance combined. Although expressed in quantities of meal they could without difficulty be converted into quantities of digestible or metabolisable energy. It seems likely that in future the scales will be expressed in terms of digestible energy, which would allow them to be applied to diets unusually low or high in energy concentration.

Poultry With the possible exception of birds reared for breeding (see Chapter 15), growing poultry are normally fed to appetite, and feeding standards for them are therefore expressed, not as amounts of nutrients, but as the nutrient proportions of the diet (Appendix Table 11).

The quantities of food eaten by poultry are inversely related to the concentration of energy in their diets. A bird changed from a diet of high to one of low energy concentration responds by eating more of the latter. In effect, it attempts to maintain its energy intake at the former level. Poultry, together with other non ruminants, are sometimes said to 'eat for calories', that is, to adjust their food intake so that their energy intake is kept at a constant level. The manner in which chicks respond to diets of differing energy content is illustrated in Table 14.6. In the experiment these results are taken from, a normal diet containing 975 kcal productive energy (or about 1430 kcal metabolisable energy) per lb was 'diluted' with increasing proportions of a low energy constituent, oat hulls. The most diluted diet had an energy concentration which was only half that of the original (and which was much lower than the range normally experienced by chicks). The chicks responded by eating up to 25 per cent more food, but even so energy intake declined by up to 29 per cent. If the energy content of a diet is increased by the addition of a concentrated source of energy such as fat, chicks respond in the opposite way. They eat less, but

the reduction in intake may be insufficient to prevent a rise in energy intake. Such differences in energy intake may have little effect on the magnitude of the liveweight increase but have a marked influence on the composition of the increase (Table 14.6).

The influence of the energy concentration of the diet on the quantities of food and of energy ingested extends also to intakes of nutrients other than those supplying energy. If the energy content of a diet is increased without change in the concentration of, for example, protein, and birds

TABLE 14.6 The Effects of Reducing the Energy Content of the Diet on the Food and Energy Intakes of Chicks and on their Growth
(After F. W. Hill and L. M. Dansky, 1954, *Poultry Sci.*, 33, 112)

	Diet No				
	1	2	3	4	5
<i>Energy content of diet</i>					
Productive energy (kcal/lb)	975	858	741	623	505
Metabolisable energy (kcal/lb)	1430	1260	1110	970	810
Metabolisable energy (per cent. of diet No. 1)	100	89	78	68	57
<i>Performance of chicks to 11 weeks of age</i> (per cent. of result for diet No. 1)					
Total food intake	100	101	113	117	125
Total metabolisable energy intake	100	90	88	80	71
Liveweight gain	100	99	102	98	98
<i>Fat content of carcass at 11 weeks of age</i> (per cent. of dry matter) (Male chicks only)	26.8	23.2	21.1	18.1	16.1

begin to eat less of the diet, then although their energy intake may remain approximately at the former level, their intake of protein will fall. The birds may then be deficient in protein. To generalise a nutrient concentration which is adequate for a diet of low energy content may be inadequate for one richer in energy. It follows that feeding standards stated as nutrient concentrations are satisfactory only when applied to diets with a particular energy concentration. The standards of Appendix Table 11 apply to diets containing 2.8 Mcal metabolisable energy per kg (1270 kcal per lb), and need to be adjusted for diets containing more or less energy. Some adjustments are discussed later in this chapter (p. 244).

Protein Requirements for Growth

Ruminants In feeding standards for growing animals, protein requirements for growth are usually incorporated into a single value for maintenance and growth combined. The factorial method of

calculating protein requirements can be used to provide this single value by including in the last equation shown on p 228 a term for the nitrogen stored by the animal. This term can be obtained from comparative slaughter trials. The equation then becomes

$$R = 6.25 \{100/B (M \times D + E + G) - M \times D\},$$

where G is the nitrogen storage (and the other symbols are as given on p 228). For example, in the Missouri 'Use of feed' experiment cattle of 800 lb liveweight gaining about 1 lb per day were found to store 0.15 lb protein (0.024 lb nitrogen) in each 1 lb of liveweight gain. A steer of this weight consuming 15 lb dry matter per day would excrete 0.020 lb endogenous urinary nitrogen per day and 0.5 lb metabolic faecal nitrogen for each 100 lb food dry matter. If the biological value of its food protein is assumed to have the average value for ruminants of 70, then its requirement of digestible crude protein for maintenance plus 1 lb of liveweight gain per day would be calculated as follows

$$\begin{aligned} R &= 6.25 \{100/70 (0.5 \times 0.15 + 0.020 + 0.024) - 0.5 \times 0.15\} \\ &= 0.59 \text{ lb DCP per day} \end{aligned}$$

As mentioned previously, factorial estimates of protein requirements often fail to agree with those determined in other ways. Protein requirements may also be assessed from the results of feeding trials in which animals are fed on rations supplying differing amounts of protein and their responses measured in terms either of liveweight gain or of nitrogen retention. In such trials rations supplying equally liberal quantities of energy, minerals and vitamins, and varying but more restricted quantities of protein, are compared, the minimum protein level giving maximum growth or nitrogen retention is taken as the estimate of the requirement. An example of such a nitrogen balance trial is shown in Fig 14.6. Calves were fed on rations supplying from 93 to 230 g digestible crude protein per day, and maximum nitrogen retention was achieved with a minimum intake of about 190 g digestible crude protein per day.

For many years the key figure in the standards for cattle given in *Rations for Livestock* has been 1.5 lb protein equivalent per day for animals of 840 lb or more and gaining around 2 lb per day, this is equivalent to about 1.7 lb digestible crude protein per day. It is about twice as high as factorial estimates of requirement, and has been much criticised in recent years. The standards given at the end of this book (Appendix Table 8) are those which were suggested by J. H. B. Roy

at a conference on feeding standards held in 1958 (see 'Further Reading' at the end of this chapter) They are based mainly on the results of feeding trials and are much lower than the *Rations for Livestock* values, but they are still higher than those calculated factorially Thus, the daily requirement of an 800 lb animal gaining 1 lb per day was earlier calculated factorially to be 0.59 lb digestible crude protein, whereas the value given in Appendix Table 8 is 0.90 lb

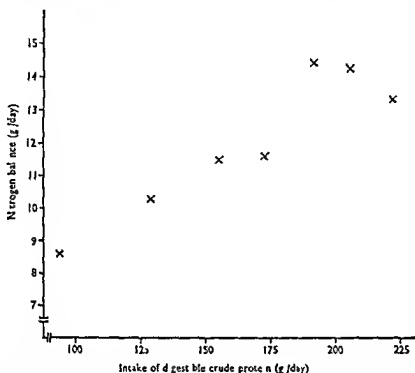


FIG 14.6 Determining the protein requirements of calves of 110 lb liveweight and gaining about 0.8 lb per day from their nitrogen balance (Plotted from the results of F. G. Whitelaw, T. R. Preston and R. D. Ndumbe 1961 *Anim. Prod.* 3, 121)

Some of the disagreement between 'theoretical' (factorial) standards and 'practical' ones may be due to the influence of the protein content of the diet on its acceptability to the animal. Diets containing theoretically adequate quantities of protein may prove inadequate in practice if their protein content is so low as to make them unacceptable to the animal. If food consumption is less than anticipated, then intakes not only of protein but also of energy and other nutrients become insufficient to produce the growth expected. Unfortunately the connection between the protein content of diets and their acceptability is not fully understood. While a low protein content may affect 'palatability', meaning the taste of the food, it may also reduce the efficiency of digestion in the rumen and so retard the rate at which food can be dealt with by the digestive tract.

Pigs and Poultry In addition to a general need for protein, non-ruminant animals have specific dietary requirements for ten or so essential amino acids. During the past 20 years many experiments have been carried out to determine quantitative requirements for essential amino acids, and there is now an increasing tendency for feeding standards expressed in terms of total protein to be supplemented by standards for all or some of these amino acids. Indeed the standards for poultry recently published in the United Kingdom by the Agricultural Research Council (see Appendix Table 11) give requirements for essential amino acids alone, it being assumed that a diet which supplies adequate amounts of these will provide sufficient total protein. For pigs, however, a requirement for total protein is still stated (Appendix Table 10), since the requirements of this species for essential amino acids are probably less well established than are those of the chick.

The requirement of pigs for total protein is most commonly determined from feeding trials where diets with different protein contents are given and growth is measured. The requirement is stated in the form of the percentage of crude protein needed in the diet, which implies that, if it is to be equally applicable when differing diets are used, the efficiency with which food proteins are digested and utilised should not vary much from one diet to another. For the diets most commonly given to pigs the protein digestibility is probably reasonably constant, but there is unlikely to be such uniformity in the efficiency with which absorbed amino acids are utilised. As shown earlier, the biological value of protein varies considerably from one food to another, that for fish meal (80), for example, being considerably higher than that for the vegetable protein concentrate, groundnut meal (60). While the range in biological value for mixed diets is narrowed by the complementary effects due to mixing proteins, it is unlikely that rations based respectively on fish meal or groundnut meal and supplying equal quantities of crude protein will also be equal in respect of the amino acids they provide.

There is therefore a danger that standards devised from diets whose protein was, perhaps, of average biological value, will be too low for application to diets containing poorer quality protein and excessive for those with better quality. The greater danger of there being insufficient protein may be avoided by setting the standards high, at a level appropriate to diets of poorer quality protein, and this in fact is what has often been done. A common standard for pigs from 50 to 100 lb liveweight is 18 per cent crude protein in the diet, but it has been shown

that if, as is usual, the diet contains the good-quality proteins of fish meal, a level of 14 per cent. crude protein is adequate.

Standards expressed as total protein alone are therefore of only partial value in the feeding of pigs (and poultry) unless there is some stipulation as to the protein quality of the diet. In pig diets, protein quality is often limited by deficiencies of one or two of the essential amino acids, and if standards for total protein are accompanied by standards for these acids, they become much more meaningful. In addition, qualifying a standard for total protein by stating that certain proportions of it must be in the form of these critical amino acids may allow the standard to be set at a lower level than formerly.

The requirements of pigs and poultry for essential amino acids. The requirement for an essential amino acid is assessed by giving diets containing different levels of the acid in question but equal levels of the remaining acids, and measuring growth or nitrogen retention. Diets differing in their content of just one amino acid may be prepared from foods naturally deficient in it, to which are added graded amounts of the pure acid. Fig. 14.7 shows the outcome of an experiment with chicks in which a diet low in lysine was supplemented in this way so as to give diets ranging in lysine content from 0.7 to 1.4 per cent. The lysine requirement of the chick was concluded from this experiment to be 1.1 per cent. of the diet. In other experiments it has been found more convenient to use synthetic diets in which much or all of the nitrogen is in the form of the pure amino acids.

Standards for the essential amino acid requirements of chicks, turkey poults and young pigs have now been devised, and some of these are given in Appendix Tables 10 and 11. At present they must be regarded only as approximate standards, for there are considerable complications to defining requirements for amino acids. Thus requirements are influenced by interactions among the essential amino acids themselves, between essential and non-essential acids and between amino acids and other nutrients. For chicks, the requirement for glycine is increased by low concentrations in the diet of methionine, arginine or B-complex vitamins. Interactions may be due to the conversion of one amino acid into another. If cystine is deficient in the diet it is synthesised by the animal from methionine; the requirement for methionine is therefore partially dependent on the cystine content of the diet, and the two acids are usually considered together. Phenylalanine and the non-essential acid, tyrosine, have a similar relationship.

Further complications are introduced by relationships between

amino acid requirements and the total protein content of the diet. If the latter is altered to compensate for a change in energy content, then the amino acid requirements will change also. For methionine the requirement appears to bear a fixed relation to total protein, and if the content of the latter is increased by 20 per cent the requirement for methionine will rise by the same proportion. The level of lysine required, however, does not show the same proportionality to total protein and energy levels. When the metabolisable energy content of

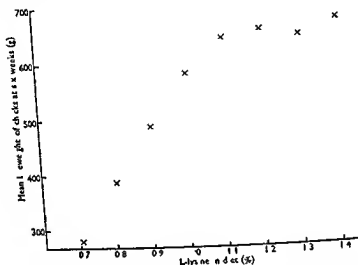


FIG 14.7 Growth of chicks given diets containing different levels of lysine (Plotted from the data of H. M. Edwards, L. C. Norris and G. F. Heuser 1956 *Poultry Sci.* 35, 385)

chick diets is 1300 kcal per lb, the requirement for lysine is 1 per cent of the diet, but when the former increases by 25 per cent to 1650 kcal, the latter increases by only 20 per cent to 1.2 per cent of the diet.

Some sort of check can be applied to values for essential amino acid requirements by comparing them with the amino acid composition of tissue proteins. The comparison cannot be expected to give complete agreement in respect of the relative amino acid proportions of food and of tissue proteins, if only because amino acids are required for purposes other than the growth and maintenance of the latter. Even so, Table 14.7 shows that for about half the essential amino acids the agreement is quite close. For the remainder it is less close, but the apparently low requirements for arginine and glycine by the chick can be explained by the limited amount of synthesis of these acids which is undertaken by the body.

The application in feeding practice of standards for as many as ten or eleven amino acids is likely to be rather laborious. How necessary is it, then, to consider all of them when devising diets for pigs and poultry? In theory there is almost unlimited scope for adjusting the proportions of dietary constituents (including synthetic acids) until the essential amino acid contents of the diet exactly equal those demanded by the standards. In practice it is usually found that the amino acid

TABLE 14.7 A Comparison of the Essential Amino Acid Proportions of the Tissue Proteins of Chicks with their Dietary Requirements for these Acids

Amino Acid	(g amino acid per 100 g protein)	
	Proportion of tissue proteins *	Proportion of dietary proteins †
Arginine	6.71	6.0
Histidine	1.96	1.75
Isoleucine	4.12	2.5
Leucine	6.63	7.5
Lysine	7.46	5.0
Methionine+cystine	3.51	3.5
Phenylalanine+tyrosine	6.43	6.0
Threonine	4.02	2.75
Tryptophan	0.77	0.75
Valine	6.72	4.0
Glycine	10.09	5.0

* H. H. Williams *et al.*, 1954, *J. biol. Chem.*, 208, 277

† Calculated on the basis of a diet containing 20 per cent protein from the requirements suggested in Appendix Table 11, for all acids except arginine. The value for arginine has been taken from the United States National Research Council's standards.

mixtures provided by the diet are out of proportion, and hence inefficiently utilised, because one or two amino acids are very markedly deficient. In consequence, the degree of success achieved in applying the standards depends particularly on whether or not the requirements of these 'limiting' amino acids are met. By comparing requirements for amino acids with the amino acid contents of typical diets, it can be shown that for pigs the acid likely to be most deficient is lysine. For chicks the 'first-limiting' amino acid is most commonly methionine, although lysine and perhaps arginine may also be deficient.

In practice therefore it may be sufficient to ensure that diets for pigs and poultry contain, first, adequate total protein, and second, adequate contents of those amino acids most likely to be deficient. When this simplification is made, however, it should be remembered that, for pigs at least, standards for total protein have often been

set high in order to be adequate for diets containing low-quality protein, i.e. for diets most deficient in the more frequently limiting amino acids. If more attention is paid to these amino acids it seems likely that standards for total protein will be reduced, bringing into prominence other amino acids which are not at present regarded as likely to be near the borderline of adequacy.

Nutrient Requirements for Wool Production

The weight of wool produced by sheep varies considerably from one breed to another, and an average value is useful only as an example. For an example we shall take a fleece of 7 lb, this representing the annual production of a sheep weighing 140 lb. Such a fleece would contain about 5 lb of actual wool fibres, the remaining 2 lb being wool wax, suint and dirt. Wool wax is produced by the sebaceous glands, and consists mainly of esters of cholesterol and other alcohols with the acids normally found in glycerides and other aliphatic acids. Suint, the secretion of the sudoriferous glands, is a mixture of inorganic salts, potassium soaps and potassium salts of lower fatty acids.

The wool fibres consist almost entirely of the protein, wool keratin. To grow in one year a fleece containing 5 lb of protein, a sheep would need to deposit daily an average of about 6 g protein or 1 g nitrogen. If this latter figure is compared with the 8 g nitrogen or thereabouts which a sheep of 140 lb might lose daily as endogenous urinary and metabolic faecal nitrogen, it will be seen that in proportion to its requirement for maintenance the sheep's nitrogen requirement for wool growth may be quite appreciable. These figures however do not tell the whole story, since the efficiency with which absorbed amino acids are used for wool synthesis is likely to be much less than that with which they are used for maintenance. Keratin is characterised by its high content of the sulphur containing amino acid, cystine, which although not an essential amino acid is synthesised from the essential acid, methionine. The efficiency with which food protein can be converted into wool is therefore likely to depend on their respective proportions of cystine *plus* methionine. Keratin contains 10-12 per cent of these acids, compared with the 2-3 per cent found in plant proteins and in the microbial proteins synthesised in the rumen, and so the biological value of food protein for wool growth is likely to be not greater than 30 per cent.

In contrast to the requirements of protein for wool growth, those of energy seem likely to be relatively smaller. In producing a fleece of 7 lb the sheep would retain about 45 kcal per day. In comparison with

its fasting metabolism of about 1200 kcal per day, this is quite small (though the efficiency with which metabolisable energy can be transferred to wool is not known).

There are no feeding standards for wool growth alone, but allowances for maintenance are set sufficiently high to provide for wool production. While nutrient requirements for wool production are, even for protein, quantitatively small, it must not be supposed that maximum wool growth will take place at a level of nutrition only slightly above the maintenance level. Wool growth reflects the general level of nutrition of the sheep. At sub-maintenance levels, when the sheep is losing weight, its wool continues to grow, although slowly. As the plane of nutrition improves and the sheep gains in weight, so wool growth too increases. There appears to be a maximum rate of growth for wool, varying from sheep to sheep within a range as great as 5 to 40 g per day. It was at one time considered that the rate of wool growth depended on protein intake, or, more specifically, on the concentrations of amino acids in the fluid bathing the wool follicles. From more recent experiments however it appears that if the sheep's diet contains a minimum of 8 per cent. crude protein, the quantity of wool it produces is related more closely to its energy than to its protein intake.

Wool quality is influenced by the nutrition of the sheep. High levels of nutrition increase the diameter of the fibres, and it is significant that the finer wools come from the nutritionally less favourable areas of land. Periods of starvation may cause an abrupt reduction in wool growth; this leaves a weak point in each fibre and is responsible for the fault in fleeces with the self-explanatory name of 'break'. An early sign of copper deficiency in sheep is a loss of 'crimp' or waviness in wool; this is accompanied by a general deterioration in quality, the wool losing its elasticity and its affinity for dyes being reduced.

MINERAL AND VITAMIN REQUIREMENTS FOR MAINTENANCE AND GROWTH

This section is concerned with the general principles governing the determination of feeding standards for minerals and vitamins. No attempt is made to discuss individual nutrients, since to do so would result in duplicating the material of Chapters 5 and 6.

Minerals

Animals deprived of a dietary supply of mineral elements continue to excrete these nutrients. Those elements which occur in the body mainly

as constituents of organic compounds, such as the iron of haemoglobin and the iodine of thyroxine, are released from these compounds when they are expended or 'worn out'. To a variable but often large extent the elements so liberated are re utilised, but re utilisation is never complete and a proportion of each mineral will be lost from the body in the faeces and urine and through the skin. Of those elements which occur in inorganic forms, such as calcium, sodium, potassium and magnesium, there are losses in the urine such as those arising from the maintenance of the acid base balance of the animal, and losses in the faeces occurring through secretions into the gut which are not re-absorbed. Because they suffer all these endogenous losses, animals require minerals for maintenance.

Endogenous losses of minerals are often small, however, in relation to the mineral content of the body. A pig of 70 lb, whose body contains about 230 g calcium, suffers endogenous losses amounting to 0.7 g of the element per day, and thus needs to replace daily about 0.3 per cent of its body calcium. The same pig contains about 40 g sodium and needs to replace 0.036 g or 0.09 per cent each day. In contrast, the pig would need to replace about 0.7 per cent of its body nitrogen each day.

The approaches used in assessing requirements for minerals are the same as those used in determining standards for energy and protein. A 'theoretical' approach is provided by the factorial method, and 'practical' estimates of requirement by balance and growth trials. Since the mineral contents of foods are expressed as the total or gross amounts present, requirements are stated in the same terms. The standards must therefore make allowance for the differences in mineral availability that occur between different species and age classes of animal (see Chapter 10).

Factorial estimates of mineral requirements The net requirement of a mineral element for maintenance *plus* growth is calculated as the sum of the endogenous losses and the quantity retained. To determine the dietary requirement, the net requirement is divided by an average value for availability (expressed as a decimal). For example, a heifer of 700 lb liveweight gaining 1 lb per day might have endogenous losses of calcium of 5 g per day and retain 3 g per day, its net requirement would therefore be 8 g calcium per day. For an animal of this weight an average value for the availability of calcium would be about 40 per cent, and the animal's dietary requirement for calcium would therefore be $8/0.4 = 20$ g per day.

The difficulties involved in the factorial approach to mineral

requirements are the same as those associated with factorial estimates of protein requirement. While the mineral composition of liveweight gains may readily (if laboriously) be determined by carcass analysis, the assessment of endogenous losses, and hence also of availability, is more difficult. Diets for ruminants which are completely free of an element are particularly difficult to prepare. Perhaps because of these difficulties of technique, theoretical estimates of mineral requirements often do not agree with practical estimates.

Growth and balance trials. When mineral requirements are assessed by comparing the effects on the animal of diets supplying different quantities of an element, the great problem is to establish a satisfactory criterion of adequacy. That intake which is sufficient to prevent clinical signs of deficiency may be insufficient to support maximum growth. Of the bone-forming elements, the intake which gives a maximum rate of liveweight gain may yet be inadequate if judged by the strength of bone produced. The position is further complicated by the mineral reserves of the animal. If these are large at the beginning of an experiment of short duration, they may be sufficient to allow normal health and growth even if the diet is inadequate, and it is therefore desirable that mineral balance should be determined directly or assessed indirectly by analysis of selected tissues. Even balance trials however may be difficult to interpret, since if the element is one for which the animal has great storage capacity, a dietary allowance which promotes less than maximum retention may still be quite adequate. In long-term experiments, then, such as those continuing for one or more annual cycles of the dairy cow, health and productivity alone may provide reliable indications of minimum mineral requirements. For growing animals on the other hand trials must usually be of shorter duration, and measurements of liveweight gain should be supplemented by measurements of mineral retention.

Present standards. The requirements for minerals given in the Appendix Tables have been derived by factorial calculation. For all species the elements which have been the subject of most investigation have been calcium and phosphorus, these being the elements most likely to be deficient in the diet. *Net* requirements for calcium and phosphorus, relative to requirements for other nutrients, tend to decline as the animal ages and bone growth slows down, but *dietary* requirements decline less with age because the availability of these elements is reduced as the animal matures. It should be noted that within small ranges in weight mineral requirements are considered to be proportional to liveweight, not to metabolic liveweight.

Vitamins

There are no endogenous losses on which to base factorial estimates of vitamin requirements, and standards must therefore be derived from the results of feeding trials. As in the assessment of mineral requirements, it may be difficult in these trials to select the criteria by which the allowances compared are judged adequate or inadequate. The main criteria are again growth rate and freedom from signs of deficiency, deficiency being detected either by visual examination of the animals or by physiological tests such as determination of the vitamin levels in the blood. Vitamin storage may also be assessed, either from actually analysing tissues or from such indirect evidence of tissue saturation as is provided by excretion of the vitamin in the urine.

TABLE 14.8 The Vitamin A Requirement of Calves
(From the data of J. M. Lewis and L. T. Wilson, 1945, *J. Nutr.*, 30, 467)

Minimum requirement for	Vitamin A (I.U./kg liveweight/day)
Prevention of night blindness	32
Optimal growth	64
Limited storage of vitamin A	250
Maximal blood level of vitamin A	500

The difficulties involved in assessing requirements are illustrated in Table 14.8, which shows that the apparent requirement can vary widely according to the criterion of adequacy preferred.

In practice, vitamin allowances must be at least high enough to prevent signs of deficiency and not to restrict the rate of growth. Higher allowances, which promote storage or higher circulatory levels of the vitamin, are justifiable only if they can be shown in the long term to influence the health and productivity of animals in a way which does not become apparent in the short-term experiments by which requirements must often be assessed. Some storage can be justified, since in most animals there may be fluctuations in both the need for the vitamins and the supply of them, and allowances are usually set at levels permitting the maintenance of stores.

Requirements for the fat-soluble vitamins, in older animals at least, are considered to be proportional to body weight. Those for the B group however, which are more intimately concerned with metabolism, vary with food intake in general, or in some cases with intake of specific nutrients. Thus the requirement for thiamine, which is particularly concerned with carbohydrate metabolism, varies according to the relative importance of carbohydrate and fat in the diet.

For similar reasons riboflavin requirements are increased by a high protein intake. Requirements vary also according to the extent to which B vitamins are synthesised in the alimentary tract. In herbivores sufficient synthesis occurs to make the animal independent of dietary supplies. In pigs and poultry considerable synthesis takes place in the lower gut, but the vitamins produced may fail to be absorbed, the contribution of the intestinal synthesis may then depend on whether the animals are free to practise coprophagy (the eating of faeces). A final point of importance concerns the availability of vitamins. Requirements are often determined from diets containing synthetic sources of the vitamins, whose availability may well be higher than that of the vitamins of natural foods. Although little is known about vitamin availability, a well documented instance of non-availability is provided by the nicotinic acid of cereals, some of which is in a bound form not available to pigs.

FURTHER READING

- H. H. MITCHELL, 1962, 1964 *Comparative Nutrition of Man and the Domestic Animals* (2 vols.) Academic Press, New York and London
S. BRODY, 1945 *Bioenergetics and Growth* Reinhold, New York
Scientific Principles of Feeding Farm Livestock, 1958 Farmer and Stockbreeder Publications Ltd, London
Also the publications referred to in the Appendix, particularly Nos 1, 2, 3, 4, 8-12 and 19

FEEDING STANDARDS FOR REPRODUCTION AND LACTATION

REPRODUCTION

It is convenient to divide reproduction into two phases. The first phase, which is important in both sexes, comprises all events leading up to conception, while the second phase is the period of pregnancy. The first part of this section is concerned with the effects of nutrition on the production of ova and spermatozoa. Nutrient requirements for these processes in mammals are small compared with the requirements for egg production in birds, and the feeding of laying poultry is therefore dealt with separately in the second part. The final part of this section is devoted to the nutrition of pregnant animals.

The anatomy of the reproductive organs and the physiology of reproduction are considered to be outside the scope of this book, but such information can be found in some of the books listed at the end of this chapter.

Two general points regarding nutrition and reproduction may be made at this stage. The first is that many of the effects of nutrition on reproductive performance are transmitted via the endocrine system, particularly via the hormones produced in the anterior pituitary. In a few instances the effect of a dietary deficiency can be related directly to a reduced output of a particular hormone, and will be corrected as successfully by hormone therapy as by improving the diet. In others the involvement of the endocrine system is less easily demonstrated, the effect on reproduction may be a consequence of a change in the rate at which a hormone is destroyed rather than the rate at which it is secreted, or of an altered sensitivity to the hormone in the organ responding to it.

The second general point is that in farm animals the effects of nutrition on reproduction are known only very imperfectly. The research needed is difficult to carry out because the response to a diet is often slow to develop, and experiments must therefore be of long duration, perhaps several generations. Many animals may

be needed if, for example, the fertility of a number of bulls has to be tested by mating each to 10–20 cows.

THE EFFECTS OF NUTRITION ON THE INITIATION AND MAINTENANCE OF REPRODUCTIVE ABILITY

Puberty in cattle is markedly influenced by the level of nutrition at which animals have been reared. In general terms, the faster an animal grows, the earlier will it reach sexual maturity. In cattle, puberty occurs at a particular liveweight or body size rather than at a

TABLE 15.1. Age and Size at Puberty of Holstein Cattle reared on Different Planes of Nutrition

Sex	Plane of nutrition (per cent. of accepted standard for TDN)	At puberty		
		Age (weeks)	Weight (lb)	Height at withers (in.)
Females *	High (129)	37.4	595.5	42.7
	Medium (93)	49.1	596.6	44.3
	Low (61)	72	531.8	44.6
Males †	High (150)	37	644	45.8
	Medium (100)	43	578	45.6
	Low (66)	51	519	44.7

* From A. M. Sorenson *et al.*, 1959, *Bull. Cornell Univ. agric. Exp. Stn.* No. 936.

† From R. W. Bratton *et al.*, 1959, *Bull. Cornell Univ. agric. Exp. Stn.* No. 940.

fixed age. This is illustrated in Table 15.1, which shows the effects of three planes of nutrition on the initiation of reproductive ability in dairy cattle. Although in both sexes there were considerable differences in age at puberty between the three treatments, differences in liveweight and in body size (as reflected in the measurement of height at withers) were much smaller.

In sheep too, a high plane of nutrition advances puberty, for ewe lambs fed liberally come into heat sooner in the breeding season and at a greater liveweight.

In pigs, on the other hand, high planes of nutrition in both sexes result in greater weights at puberty, but have little effect on age at puberty. Indeed very high levels of feeding, which induce excessive fatness, may actually delay the initiation of reproductive ability.

In practice, the factor which decides when an animal is to be first used for breeding is body size, and at puberty animals are usually

The evidence for a causative association between overfeeding and impaired reproductive ability is less convincing. Very fat animals frequently are sterile, but the two conditions, fatness and sterility, may both be effects of, for example, an endocrine disturbance, rather than one the cause of the other. Fatness and sterility occur together most commonly in sows, and also occur together frequently in show animals. Over fat sows may continue to produce ova while failing to show signs of oestrus, it has been suggested that the oestrogens intended to be responsible for the latter are absorbed in the fat depots.

Effects of Specific Nutrient Deficiencies on the Production of Ova and Spermatozoa

So far this chapter has been concerned with the effects upon reproduction of variations in quantity of food, effects which in many cases are responses to variations in the supply of energy. Attention will be given in this section to the effects on reproduction of deficiencies, or excesses, of specific nutrients.

Little is known about the influence on reproduction in farm animals of a deficiency of protein. One reason for this is that protein deficiency, because it depresses appetite, is frequently complicated by deficiencies of other nutrients. Protein has been studied more extensively with laboratory animals, where its deficiency eventually leads to reproductive failure. In general the effects of protein deficiency on reproduction appear to be much more severe in growing than in mature animals.

When deficiencies of minerals or vitamins occur in breeding animals, the general signs of deficiency described earlier (see Chapters 5 and 6) usually appear before reproductive ability is seriously affected. In other words, reproductive function is more resistant to these deficiencies than are other bodily activities. The effect of vitamin A deficiency illustrates this point, for although such a deficiency ultimately causes complete failure of reproduction, animals blinded by the deficiency may still be capable either of producing semen or of conceiving. Prolonged deficiency leads eventually in males to degeneration of the testes and in females to keratinisation of the vagina.

Deficiency of vitamin E has a profound effect on reproduction in rats, but the evidence suggests that the vitamin does not play any appreciable role as a cause of infertility in cattle and sheep. In pigs however it has been reported that vitamin E deficient diets may result in lowered reproductive performance. There is also evidence from experiments with mature fowls that a prolonged vitamin E deficiency results in sterility in the male and reproductive failure in the female,

and in the male the sterility may become permanent through degenerative changes in the testes.

Of the mineral elements, both calcium and phosphorus are important in reproduction, although of the two it is phosphorus whose deficiency is more commonly associated with reproductive failure. (In females this failure may sometimes, but not always, be due to oestrus not taking place.) Phosphorus deficiency arises most commonly in ruminants grazing on herbage deficient in the element, and in such circumstances the failure of reproduction occurs in conjunction with the general signs of phosphorus deficiency described earlier. When low-phosphorus diets have been used in experimental studies, however, there have been cases where reproduction was impaired in animals that were normal in other respects. In sows, manganese deficiency has been shown to interfere with reproduction. A complex interaction between manganese, calcium and phosphorus has therefore been suggested as influencing reproduction in cattle.

EGG PRODUCTION

Rearing of Hens

Birds intended for egg production are commonly fed to appetite during the rearing period, but in recent years the possibilities of restricting food intake have been investigated. Restriction during the rearing period, to 70-80 per cent. of what would be consumed voluntarily, appears to delay the onset of egg production and to retard growth; the practice is also associated with a higher mortality during rearing. However if such restricted birds are subsequently, during the laying period, fed to appetite, they appear to compensate for many of the earlier disadvantages. Once they begin to lay they produce eggs at a slightly faster rate than birds previously fed to appetite, and they make up their liveweight deficit. In many cases mortality is lower among layers which have been reared on a restricted regime than among those birds fed on a normal diet, presumably because more of the weaker birds do not survive during rearing.

Birds reared on a restricted intake naturally yield a saving in food, but they may almost nullify this by eating more food at the beginning of the laying period. One definite advantage of feed restriction is a decrease in number of small eggs laid.

Nutrient Requirements of Laying Hens

Good flocks of layers produce an average of 210-220 eggs per bird per year. Their eggs weigh on average 2 oz (57 g) and have the chemical

composition shown in Table 15 2, and an energy value of about 90 kcal. In theory this information could be used as the basis for a factorial calculation of the nutrient requirements of layers, but it is doubtful whether sufficient information exists on the efficiency with which nutrients are transferred from food to egg to enable such a calculation to be made. At one time, laying hens were rationed according to a system in which they were given so much food per day for maintenance

TABLE 15 2 Average Composition of the Hen's Egg

		Whole egg (including shell)	Edible parts only
(a) Gross constituents (per cent)			
Water		65.6	73.6
Protein		12.1	12.8
Lipids		10.5	11.8
Carbohydrate		0.9	1.0
Ash		10.9	0.8
(b) Major mineral elements (g per egg)			
Ca	2.0		
P	0.12	K	0.07
Mg	0.03	Na	0.07
Cl	0.09	S	0.11
(c) Trace mineral elements (mg per egg)			
Fe	1.6		
I	0.007		
Cu	0.09		
Mn	0.015		

and so much for the estimated egg production, but today they are almost invariably fed to appetite. Feeding standards for layers, as for other classes of poultry, are therefore expressed in terms of nutrient proportions rather than quantities. The requirements of layers are shown in Appendix Table 11.

Energy The values given in Appendix Table 11, except where otherwise stated, relate to diets containing 2 g Mcal/kg or 1270 kcal/lb of ME. Like younger birds, the hen maintains an approximately constant energy intake by eating more of low- and less of high energy diets, and in order to keep her intake of protein and other nutrients constant it is necessary to adjust the composition of any diets containing more or less metabolisable energy than 1270 kcal/lb so that the ratios of these nutrients to energy are maintained.

Although the hen has this ability to adjust her intake of food to satisfy her energy requirements, her adjustments in intake may not

compensate for the changes in energy concentration completely. With diets very low in energy there is likely to be a reduction in total energy intake, while with exceptionally energy-rich diets total intake will be increased. High intakes of energy may have the advantage of increasing egg weight, but they may also lead to an excessive deposition of fat in the hen herself.

The energy requirements for both maintenance and production are given in the first part of Appendix Table 11. The energy required for the production of one 'standard' (2 oz) egg is 122 kcal, and the values in Table 11 have been calculated using this value. For example, a hen of 6 lb would require 335 kcal metabolisable energy per day for maintenance. If her production rate were 70 per cent (5 eggs per week), her total daily requirement for energy would be

$$335 + 70/100 \times 122 = 420 \text{ kcal ME}$$

A requirement of 122 kcal ME for the production of a 90 kcal egg implies an efficiency of conversion of metabolisable energy of about 74 per cent.

Protein Laying hens need relatively less protein than growing poultry. Their essential amino acid requirements are not completely known, because only recently has it been found possible to maintain egg production in layers given their protein as mixtures of pure amino acids, the amino acids investigated have therefore been those in which natural foods are deficient. The amino acid requirements of layers and chicks are compared in Table 15.3.

Mineral elements Laying hens have a high requirement for calcium because of the large amount of this element in the eggshell. It is difficult to obtain reliable estimates of phosphorus requirements because of the problem of the availability of phytate phosphorus (see Chapter 6), in Appendix Table 11 the phosphorus requirement is therefore expressed as inorganic phosphorus to be added to the diet. Other elements which are likely to be deficient in normal diets are sodium, chlorine, iron, iodine, manganese and zinc.

Common salt is generally added to the diet of laying hens and is beneficial in counteracting cannibalism and feather picking. The requirement of poultry for sodium is met by the provision of 0.4 per cent of salt in the diet. In excessive amounts salt is definitely harmful, although adult birds can withstand 20 per cent in the diet if adequate drinking water is available. The iron content of the egg is relatively high (see Table 15.2), and consequently the requirement of the laying hen is large compared with the requirement for maintenance. Excessive

iron in the diet is, however, harmful and may give rise to rickets by rendering the phosphorus of the diet unavailable. Iodine and manganese are particularly important for breeding hens, since a deficiency of either leads to a reduction in the hatchability of eggs, and may also reduce the viability of the chicks after hatching. The requirements for manganese are influenced by breed differences as well as by the levels of calcium and phosphorus in the diet, this trace element is more likely

TABLE 15.3 Amino Acid Requirements of Chicks and Laying Hens
(expressed as Percentages of Total Protein)

<i>Amino acid</i>	<i>Young chick</i>	<i>Laying hen</i>
Arginine	4.0	
Histidine	1.8	
Lysine	5.0	3.3
Tryptophan	0.8	0.9
Methionine + cystine	3.5	3.7
Phenylalanine + tyrosine	6.0	4.7
Leucine	7.5	4.7
Isoleucine	2.5	3.3
Valine	4.0	3.7
Threonine	2.8	2.7
Glycine	5.0	
Approximate protein level (per cent)	20	15

to be deficient in diets predominantly rich in maize than in those based on wheat or oats. Zinc deficiency in the diet of laying hens adversely affects egg production and hatchability, and results in the production of weak chicks with a high mortality rate. In the past it is possible that the use of galvanised feeding and drinking troughs was an important source of this element.

Vitamins An important feature of the vitamin requirement of laying hens is that the minimum amounts required to ensure maximum egg production may be insufficient to provide for the normal growth of the chick, both before and after hatching. Requirements for some vitamins are not yet known, but it appears that for at least riboflavin, pantothenic acid, folic acid and vitamin B₁₂ the quantities needed for maximum hatchability are appreciably greater than those for egg production alone. For vitamins A and D this is not so.

The value of β carotene as a source of vitamin A for poultry depends upon a number of factors, and it has been suggested that in practice this provitamin should be considered as having, on a weight basis, only one sixth of the value of vitamin A.

Regarding vitamin D, it should be remembered that D₃ (cholecalciferol) is 35 times as potent for poultry as D₂ (ergocalciferol)

REQUIREMENTS FOR PREGNANCY

Growth of the Foetus

The growth of the foetus (or embryo) is accompanied by the formation of the membranes associated with it, and also by considerable enlargement of the uterus. The quantities of nutrients deposited daily in the uterus and its contents may be determined by weighing and analysing

TABLE 15.4 Deposition of various Nutrients and Energy in the Uterus and Mammary Gland of the Cow at different Stages of Pregnancy
(From values and equations given by J. Moustgaard, 1959, in *Reproduction in Domestic Animals* (ed. H. H. Cole and P. T. Cupps), 2 vols. Academic Press, New York and London)

Days after conception	Deposited in uterus (per day)				Deposited in mammary gland Protein (g/day)
	Energy (kcal)	Protein (g)	Calcium (g)	Phosphorus (g)	
100	40	5	—	—	—
150	100	14	0.1	—	—
200	235	34	0.7	0.6	7
250	560	83	3.2	2.7	22
280	940	144	8.0	7.4	44
(Approx. net daily requirement for maintenance of 1000-lb cow)	(7000)	(300)	(8)	(12)	

uteri taken from animals killed at various stages of pregnancy. The results of such investigations with cows are shown in Fig. 15.1 and Table 15.4. (The values in Table 15.4 were obtained by the differentiation of equations fitted to the data of Fig. 15.1.)

In the early stages of pregnancy the amounts of nutrients deposited are small, and it is only in the last third of pregnancy (from the sixth month onwards in cattle) that it becomes necessary to make special provision in the diet for the growth of the foetus. Even in the later stages the net energy needed for the growth of the uterus and its contents is small in relation to the maintenance requirement of the mother herself, but net requirements for protein and for calcium and phosphorus (and other mineral elements) are quite appreciable in the last stages of pregnancy.

Mammary Development

Mammary development takes place throughout pregnancy, but it is

only in the later stages that it proceeds rapidly enough to make appreciable nutrient demands. Even then the quantities of nutrients laid down in the gland are quite small. In the heifer, for example, it has been shown by the analysis of animals slaughtered at various intervals

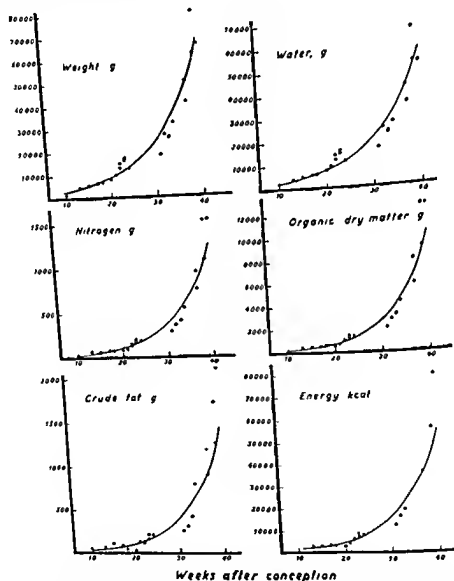


FIG 151 Weight and composition of the pregnant bovine uterus related to time after conception (From J. Moustgaard 1959, Nutrition and reproduction in domestic animals, in *Reproduction in Domestic Animals* (ed. H. H. Cole and P. T. Cupps), Vol II Academic Press, New York and London)

during pregnancy that even in the last two weeks, i.e. when mammary growth is proceeding at its fastest rate, the quantity of protein deposited daily is no more than 45 g.

Basal Metabolism during Pregnancy

The fasting metabolism of pregnant animals is often found to be greater than that of non-pregnant animals of similar weight. The difference, often called the *heat increment of gestation*, is generally attributed to a higher basal metabolism in the mother herself rather than to the heat produced by the foetus. A higher basal metabolism of the mother may be a response to changes in hormone levels during pregnancy.

The heat increment of gestation increases throughout pregnancy, and this, together with the liveweight increase which should occur, leads to a gradual rise in the maintenance energy requirement. At the end of pregnancy the energy requirement for maintenance and the growth of the foetus has been estimated in cattle to be about $1\frac{1}{2}$ times that of the non-pregnant maintenance requirement. Thus the requirement for energy in pregnancy is increased by far more than would be deduced from the storage of energy in the foetus (see Table 15.4).

Extra-uterine Growth during Pregnancy

The liveweight gains made by pregnant animals are often considerably greater than can be accounted for by the products of conception alone. For example, a litter of 10 piglets and its associated membranes may weigh 40 lb at birth, but sows frequently gain over 100 lb during gestation. The difference represents the growth of the mother herself, and sows may in their own tissues deposit 3-4 times as much protein and 5 times as much calcium as is deposited in the products of conception. This *pregnancy anabolism*, as it is called, is obviously necessary in immature animals which are still growing, but it occurs also in older animals. Frequently much of the weight gained during pregnancy is lost in the ensuing lactation.

Pregnancy anabolism is often encouraged in pigs and cattle on the grounds that it leads to higher milk yields. It is argued that in early lactation the nutrient intake may fall short of requirements and that a store of nutrients is therefore valuable at that time. It is also believed that the higher plane of nutrition required to promote gains in pregnancy is beneficial in inducing greater mammary gland development, and in accustoming the animal to the high level of feeding she will

deficiencies The ability of the foetus to make the mother anaemic has already been mentioned, this situation is unusual in farm animals because their diets are normally well supplied with iron

The foetus has a high requirement for carbohydrate, and by virtue of its priority is able to maintain the sugar concentration of its own blood at a level higher than that of the mother If the glucose supply of the mother is insufficient her blood glucose may fall considerably, to levels at which nerve tissues (which rely on carbohydrate for energy) are affected This occurs in sheep in the condition known as *pregnancy toxæmia*, which is prevalent in ewes in the last month of pregnancy Affected animals become dull and lethargic, lose their appetite and show nervous signs such as trembling and holding the head at an unusual angle, in animals showing these signs the mortality rate may be as high as 90 per cent The disease occurs most frequently in ewes with more than one foetus—whence its alternative name of ‘twin lamb disease’—and is most prevalent in times of food shortage and when the ewes are subjected to stress in the form of inclement weather or transportation Blood samples from affected animals usually show, in addition to hypoglycaemia, a marked rise in ketone content and an increase in plasma free fatty acids

There does not appear to be one single cause of pregnancy toxæmia The main predisposing factors are undoubtedly the high requirement of the foetus for glucose and possibly a fall in the carbohydrate supply of the mother, which may arise through food shortage or through a decline in appetite in late pregnancy The biochemical explanation for the disease hinges on the fact that the tricarboxylic acid cycle cannot function correctly without an adequate supply of oxalacetate, which is derived from glucose or such glucogenic substances as propionate, glycerol and certain amino acids If the oxalacetate supply is curtailed, acetyl CoA, which is derived from fats or from acetate arising through rumen fermentation, is unable to enter the cycle, and so follows an alternative pathway of metabolism which culminates in the formation of acetoacetate, β hydroxy butyrate and acetone In pregnancy toxæmia the balance between metabolites needing to enter the cycle is upset by a reduction in glucose availability and an increase in acetyl CoA production, the latter being caused by the animal having to metabolise its reserves of body fat The clinical signs can thus be attributed both to hypoglycaemia and to the acidosis resulting from hyperketonaemia An additional factor is that increased production of cortisol by the adrenal cortex in response to stress may reduce the utilisation of glucose, this possibility is supported by the

fact that byperketonaemia may continue after the blood glucose level has been restored to normal.

The disease has been treated by the injection of glucose, by feeding with substances likely to increase blood glucose levels, or by hormone therapy. Only moderate success has been achieved, however, and there is no doubt that the control of pregnancy toxæmia lies in the hands of the shepherd rather than the veterinary surgeon. The condition can be prevented by ensuring an adequate food supply in late pregnancy and by using foods which supply glucose or its precursors rather than acetate, i.e. concentrates rather than roughages.

LACTATION

We are here concerned with the nutrient requirements for milk production, which involves a conversion of nutrients into milk on a

TABLE 15.6. The Average Percentage Composition of Milks of Farm Animals

	<i>Fat</i>	<i>Solids- not-fat</i>	<i>Crude protein</i>	<i>Lactose</i>	<i>Calcium</i>	<i>Phosphorus</i>
Cow	3.6	8.7	3.3	4.7	0.13	0.09
Goat	4.5	8.7	3.3	4.1	0.13	0.11
Ewe	7.4	11.9	6.1	4.8	0.20	0.16
Sow	8.5	11.6	5.8	4.8	0.25	0.17

large scale and is a considerable biochemical and physiological achievement. A high-yielding dairy cow, for example, may in a single lactation produce as much dry matter in the form of milk as is present in her own body. The raw materials from which the milk constituents are derived, and the energy for the synthesis of certain of these in the mammary gland, are supplied by the food. The actual requirement for food depends upon the amount and composition of the milk being produced.

Qualitatively the milk of all species is similar in composition, although the detailed constitution of the various fractions such as protein and fat vary from species to species. Table 15.6 shows the average composition of milks of farm animals.

The major constituent of milk is water. Dissolved in the water are a wide range of inorganic elements, soluble nitrogenous substances such as amino acids, creatine and urea, the water-soluble protein albumin, together with lactose, enzymes, water-soluble vitamins of the B complex and vitamin C. In colloidal suspension in this solution are inorganic substances, mostly compounds of calcium and phosphorus, and the protein casein, while dispersed throughout this aqueous phase

is a suspension of minute milk fat globules. The fat phase contains the true milk triglycerides in addition to certain fat-associated substances such as phospholipids, cholesterol, the fat-soluble vitamins, pigments, traces of protein and heavy metals. The fat phase is usually referred to simply as 'fat', and the remaining constituents, other than water, are classed as 'solids not fat' or 'SNF'.

Sources of the Milk Constituents

All or most of the major milk constituents are synthesised in the mammary gland from various precursors which are selectively absorbed from the blood. The gland also exerts this selective filtering action on certain proteins, minerals and vitamins, which are not elaborated by it but are simply transferred directly from the blood to the milk.

Milk proteins About 95 per cent of the nitrogen in milk is present as protein, the remainder consisting of substances such as urea, creatine and ammonia which filter into the milk from the blood. The protein fraction is dominated by casein, which contains about 78 per cent of the total milk nitrogen, the protein in next greatest amount is β lactoglobulin. Both these proteins are elaborated in the mammary gland from amino acids absorbed from the blood and synthesised in the gland itself. The remainder of the protein fraction is made up of a small amount of albumin, pseudoglobulin and euglobulin, all absorbed directly from the blood.

Lactose With the exception of traces of glucose and galactose, lactose is the only carbohydrate in milk. Chemically a molecule of lactose is produced by the union of one glucose and one galactose residue. The mammary gland contains an enzyme system capable of changing glucose to galactose, which may then unite with glucose to give lactose. Lactose may also be synthesised from small carbon fragments in the form of acetate, but this is a minor source of the sugar.

Milk fat Milk fat is a mixture of triglycerides containing saturated acids with four to twenty carbon atoms, and a range of unsaturated acids of which the chief is oleic acid, in addition there are small amounts of the more unsaturated linoleic and linolenic acids. The amounts of the fatty acids present vary with the species of the animal, ruminants having a higher proportion of low molecular weight acids in their milk fat than simple stomached animals, as shown in Table 15.7.

The mammary gland is capable of synthesising the saturated fatty acids from acetate and β hydroxybutyrate. Such syntheses are stimulated by glucose, but this need not be present except in non ruminant

animals; glucose may serve as the sole precursor of the fatty acids in such animals. In ruminants the saturated acids of milk fat, up to and including palmitic acid, are mostly derived from acetate and β -hydroxybutyrate. About 70 per cent. of the high molecular weight acids, palmitic acid and above, are derived directly from the blood glycerides and fatty acids. The monoethenoid acids may be derived in part from analogous saturated acids or from dietary fat, but the di- and triethenoid acids are obtained only from dietary fat since they cannot be synthesised in the body.

The glycerol residue of the glycerides is obtained almost entirely from glucose, although there is a small synthesis from acetate. Some will also be available from ingested glycerides.

TABLE 15.7 Component Fatty Acids of the Milk of Various Animals
(Percentages by weight. Values derived from T. P. Hilditch and P. N. Williams, 1964, *The Chemical Constitution of Natural Fats*, 4th ed. Chapman and Hall, London)

	Saturated										Unsaturated		
	C ₄	C ₆	C ₈	C ₁₀	C ₁₂	C ₁₄	C ₁₆	C ₁₈	C ₂₀		Mono-ethenoid	Di-ethenoid	Others
Cow	4	2	1	2	3	9	25	11	1		38	4	1
Goat	3	3	3	10	6	12	28	6	1		25	4	trace
Sheep	3	3	2	5	4	10	24	13	1		29	5	2
Pig	1					2	27	7	0		45	15	4

Minerals. The inorganic elements of milk may be divided conveniently into two groups. The first comprises the major elements calcium, phosphorus, sodium, potassium, magnesium and chlorine. The second group, the trace constituents, contains some twenty-five elements whose presence in milk has been well authenticated; these include metals such as aluminium and tin, the metalloids boron, arsenic and silicon, and the halogens fluorine, bromine and iodine. Such substances are present in very small amounts, and their presence in milk is coincidental with their presence in blood; nevertheless they may have an important bearing on the nutritive value of the milk and on the health and well-being of the sucking animal. The inorganic constituents of milk are absorbed directly from the blood by the mammary gland, which shows considerable selectivity; the gland is able to block the entry of some elements such as selenium and fluorine while allowing the passage of others such as zinc and molybdenum. This selectivity may be a considerable disadvantage when it acts against

elements whose presence at increased levels in the milk may be desirable. Copper and iron, for example, are both elements important in haemoglobin formation and therefore for the nutrition of the young animal, yet despite the fact that the levels of iron and copper in milk are never adequate they cannot be raised by giving increased amounts to the lactating animal, even when blood levels of these elements are so raised. The iron content of colostrum, the milk produced in the immediate *post partum* period, may be up to fifteen times that of normal milk, but during this time transfer of substances between blood and milk is abnormal.

Vitamins. Vitamins are not synthesised in the mammary gland and those present in milk are absorbed from the blood. Milk has considerable vitamin A potency owing to the presence of both vitamin A and β carotene. The amounts of vitamins C and D present are very small, while vitamins E and K occur only as traces. There is a large range of B-vitamins in milk, including thiamine, riboflavin, nicotinic acid, B₆, pantothenic acid, biotin, folic acid, choline, B₁₂ and inositol.

It will be clear from the foregoing that the mammary gland must be provided with a wide range of materials if it is to perform its function of producing milk. Essential amino acids must be available, and either a supply of non-essential amino acids or the raw materials for their synthesis must be provided, so that synthesis of specific milk proteins may take place. In addition non-specific milk proteins must be supplied as such. Glucose and acetate are required for lactose and fat synthesis, and minerals and vitamins must be provided in quantities that allow the maintenance of normal levels of these milk constituents. The substances themselves, or the raw materials from which they are produced, have to be supplied either from the food or from the products of microbial activity in the alimentary canal.

Only in the case of the dairy cow, and to a lesser extent the goat, is sufficient information available on yield and composition of milk to allow a reliable estimation of nutrient requirements for lactation to be made. Where other animals are concerned no attempt is made to ration separately for lactation, and feeding standards are formulated for the combined functions of maintenance and lactation.

NUTRIENT REQUIREMENTS OF THE LACTATING DAIRY COW

The nutrient requirements of the dairy cow for milk production depend upon the amount of milk being produced and upon its composition.

The yield of milk is decided primarily by the breed of the cow. Generally speaking, the order of yield for the main British dairy breeds is: Friesian, Ayrshire, Shorthorn, Red Poll, Guernsey and Jersey (Table 15.8), but there are considerable intra-breed variations with

TABLE 15.8. Milk Yields of the main British Breeds of Dairy Cows
(After *Milk Marketing Board, Rep. Breed and Prod. Org.*, 1963-64, 14, 75)

Breed	Average lactation yield (lb)
Friesian	9963
Ayrshire	8826
Shorthorn	8274
Red Poll	7885
Guernsey	7747
Jersey	7351

strain and individuality. Thus certain strains and individuals of a low-yielding breed may often outyield others of a higher-yielding breed. Old cows tend to have higher yields than younger animals, but the main short-term factor affecting milk yield is the stage of lactation: yield

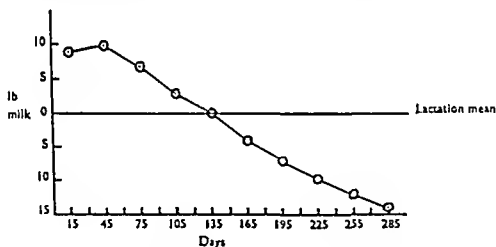


FIG. 15.2. Effect of stage of lactation on milk yield of the dairy cow.
(After R. Waite *et al.* 1956. *J. Dairy Res.* 23, 67.)

usually increases from parturition to about the middle or end of the second month and then falls regularly to the end of lactation, as is shown for Ayrshire cows in Fig. 15.2.

As a result of these factors the yield of milk may vary over a very wide range. Fortunately such variations present little difficulty in assessing the nutrient requirements of the cow, since yield is easily and conveniently measured.

The composition of milk varies with a number of non-nutritional

factors Milking technique may have a profound effect on fat content and thus on total solids content, since incomplete milking may leave a considerable volume of fat-rich residual milk in the udder. Unequal intervals between milkings may reduce fat content where a single interval exceeds sixteen hours, especially with high-yielding cows. Again, diseases, particularly mastitis, may reduce the compositional quality of milk. In a properly managed herd none of these factors should be of any importance. Certain variations in composition have to be accepted, however, since they are inevitable for a given herd. The factors responsible for these variations are breed, strain, individuality, age of cow and stage of lactation.

TABLE 15.9. Effect of Breed of Cow on the Percentage Composition of Milk

Breed	Fat	Solids-not fat	Crude protein	Lactose	Ash
Friesian *	3.49	8.59	3.28	4.46	0.75
Shorthorn *	3.56	8.71	3.32	4.51	0.76
Ayrshire *	3.72	8.78	3.38	4.57	0.74
Guernsey *	4.55	9.01	3.57	4.62	0.77
Jersey †	4.97	9.19	3.66	4.70	0.77

* After E. R. Ling, S. K. Kon and J. W. G. Porter, 1961, in *Milk: the Mammary Gland and its Secretion* (ed. S. K. Kon and A. T. Cowie), Vol. 2, p. 236. Academic Press, New York and London.

† After A. Reinart and J. M. Nesbitt, 1956, *Int. Dairy Congr. XIV*, Rome, 1, 925.

Effect of breed, strain within the breed and individuality on milk composition There is a definite breed order in relation to milk quality which is the reverse of that for milk yield. From Table 15.9 it can be seen that the Jersey produces the highest quality milk, while the high-yielding Friesian gives the poorest quality product. It is interesting to note the difference in the constitution of the solids-not-fat fraction of the different breeds, the milk from the high yielding Friesian, for example, has a proportionately higher lactose and lower protein content than the milk from the lower-yielding Jersey. As for yield, the strain and individuality of the cow have an important effect on milk composition, many Friesian cows may average more than 4 per cent of fat and 8.9 per cent of solids-not-fat over a lactation, while some Jersey cows may not match these figures. Table 15.10 shows how milk may vary in composition within breeds.

Effect of age on milk composition As the age of the cow increases, so the quality of the milk produced becomes poorer. This is shown

for Ayrshire cows in Table 15.11. The regression of solids-not-fat content on age is linear, and the decrease occurs almost equally in lactose and protein. Fat content on the other hand is relatively constant for the first four lactations, and then decreases gradually with age.

TABLE 15.10. Within-breed Variation in the Percentage Composition of Cow's Milk
(After O. R. Overman *et al.*, 1929, *Bull. Ill. agric. Exp. Stn.*, No. 325)

Breed	Fat	Solids-not-fat
Ayrshire	2.92-5.66	7.20-10.34
Guernsey	3.65-7.66	8.19-11.10
Holstein/Friesian	2.60-6.00	7.82-11.90
Jersey	3.28-9.37	7.68-11.07

The age frequency distribution of a herd may profoundly affect the average composition of the mixed-herd milk.

Effect of stage of lactation on milk composition. Advancing lactation has a marked effect on the composition of milk, which is of poorest quality during that period when yield is at its highest. Both fat and

TABLE 15.11. Effect of Age of Cow on the Percentage Composition of Milk
(After R. Waite *et al.*, 1956, *J. Dairy Res.*, 23, 65)

Lactation	Fat	Solids-not-fat	Crude protein	Lactose
1	4.11	9.01	3.36	4.72
2	4.06	8.92	3.35	4.62
3	4.03	8.82	3.28	4.59
4	4.02	8.84	3.30	4.57
5	3.90	8.72	3.26	4.53
6	3.91	8.74	3.30	4.48
7	3.94	8.67	3.25	4.48
8	3.82	8.65	3.23	4.44
9	4.03	8.70	3.27	4.48
10	3.83	8.66	3.25	4.46
11	3.77	8.61	3.16	4.46

solids-not-fat contents are low at this time, and then improve gradually until the last three months of the lactation, when the improvement is more rapid. The changes are shown for Ayrshire cows in Fig. 15.3. The changes in total solids-not-fat content are the resultant of changes in the individual constituents: ash content remains practically constant throughout the lactation; crude protein content changes with the solids-not-fat, but the changes tend to be more exaggerated; lactose content differs from that of other constituents in following the yield curve, and is at a maximum at peak yield.

It will be obvious that assessment of milk composition is a more difficult task than measurement of milk production, since there are here five main variants and the analytical work involved in their determination is considerable. Furthermore, short term variations reduce considerably the validity of such results when they become available. In evaluating milk composition, therefore, assumptions are often made concerning the quantitative relationships between constituents, which allow composition to be predicted from the content of a single easily determined constituent, usually fat.

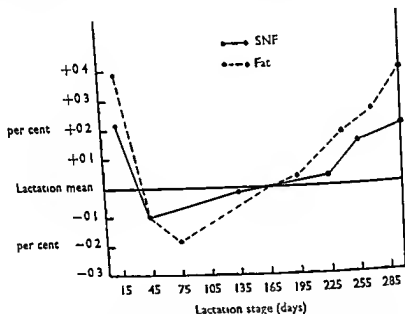


FIG 15.3 Effect of stage of lactation on milk composition of the dairy cow (After R. Waite *et al* 1956 *J Dairy Res* 23, 67)

Energy Requirements

Energy standards may be derived factorially. This involves a calculation of the gross energy value of the milk being produced, which may be used along with the yield to estimate the net energy requirement for milk production. Determination of the gross energy of milk involves either bomb calorimetry or a detailed chemical analysis; the amounts of fat, carbohydrate and protein are then multiplied by their calorific values and the products summed, as illustrated in Table 15.12. An alternative procedure is to use formulae based on statistical interrelationships between milk constituents to calculate gross energy content from the percentage of a single

constituent such as fat (F), e.g.

$$\text{kcal/kg milk} = 304.8 + 114.1 F.*$$

Using this formula and assuming a fat content of 4 per cent., we have a gross energy of 761.2 kcal/kg or 345.2 kcal/lb.

The next step in the factorial estimate is the calculation of the amount of food energy required to provide the estimated net requirement. For this the efficiency of utilisation of food energy in milk production must be known. From the calorimetric work of Forbes, Fries and Kellner, an efficiency of utilisation of metabolisable energy for milk production of about 70 per cent. is indicated. This figure is believed to apply to diets which promote a normal rumen fermentation; the

TABLE 15.12. Calculation of the Gross Energy Value of Milk

	<i>Per cent.</i>	<i>Gross energy (kcal/lb)</i>	<i>Gross energy (kcal/lb milk)</i>
Fat	4.0	4132	165.28
Protein	3.4	2658	90.37
Carbohydrate	4.7	1792	84.22
Milk			<hr/> 339.87

proportion of acetic acid in the rumen volatile fatty acids is then in the range 50-60 per cent. There is evidence however that when the proportion of acetic acid is outside this range, the efficiency of utilisation of metabolisable energy for milk production is less than 70 per cent. (Fig. 15.4). It would seem that when the proportion of acetic acid is below 50 per cent., the cow is unable to synthesise sufficient of the lower and medium-chain fatty acids which form a large part of milk fat; when there is more than 65 per cent. of acetic acid, efficiency is low as in other forms of production.

The efficiency of utilisation of metabolisable energy is influenced also by the level of protein in the diet. Where protein content is inadequate, body tissues are katabolised to make good the deficiency, a process which is wasteful of energy. Where protein content is too high, excess amino acids are used as a source of energy. Since protein is used relatively inefficiently as a source of energy for the animal, such a process reduces the overall efficiency of utilisation of metabolisable energy. The inclusion of correction factors in calculations to allow for variations in rumen volatile fatty acid patterns and protein level is not practicable, since the effects of such variations cannot be adequately

* After W. L. Gaines and F. A. Davidson, 1923, *Bull. Ill. agr. Exp. Sta.*, No. 245.

predicted Generally it is considered that the value of 70 per cent for efficiency of metabolisable energy utilisation for milk production is acceptable in practice, and may be used to calculate the energy requirement for milk production The net requirement for metabolisable energy for production of milk (4 per cent fat), assuming the gross energy value is 340 kcal per lb, is

$$\text{GE of milk} \times 100/70 = 340 \times 100/70 = 486 \text{ kcal/lb}$$

Requirements formulated as a result of feeding trials or as the result of factorial calculations are mean values, and are usually modified in their translation into feeding standards, as described in Chapter 14 Blaxter has reviewed the calorimetric work on milk production and has calculated a mean requirement of 2.67 lb starch equivalent (SE) per 10 lb of milk From the spread of the values contributing to this mean a safety margin was calculated statistically this was 0.23, giving an allowance of 2.9 lb SE per 10 lb of milk

From the experiments of Kellner and others, 1 lb starch equivalent

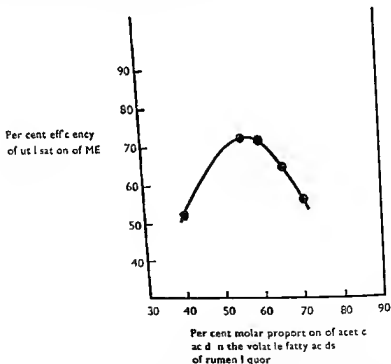


FIG 15.4 Energetic efficiency of lactation (After K. L. Blaxter 1962. *The Energy Metabolism of Ruminants*, p. 258 Hutchinson, London)

was found to supply, on average, about 1340 kcal net energy for milk production (see Chapter 12). The starch equivalent required for the production of 1 lb of milk may therefore be calculated as $340/1340 = 0.25$ lb. The standard used for many years in the United Kingdom of 2.6 lb starch equivalent per gallon of 4 per cent. fat milk, recommended by Woodman in earlier editions of *Rations for Livestock*, was derived in this way.

If a cow is supplied with energy which is theoretically sufficient for maintenance and for, say, 5 gallons of milk per day (i.e. is given a production ration supplying $5 \times 2.6 = 13$ lb SE), there is no guarantee that the animal will produce 5 gallons of milk per day. Lactating cows are usually either gaining or losing body weight. If the cow considered above were losing weight, then the animal would be making reserves of energy available to enable her to maintain her level of milk production. If on the other hand she were gaining weight, some of the production ration would be diverted from milk production for this purpose. The ability of cows to divert part of their production ration for the growth of their own tissues, or alternatively to supplement the energy available for milk production by the breakdown of these tissues, varies considerably from one individual to another; cows of high-yielding capacity would tend to use a higher proportion of a production ration for milk than would those of lower potential. Within individuals the tendency is that, as the production ration is increased, the proportion of the energy of the increment which is used for milk production decreases; in other words, the input of energy required per gallon increases as the milk yield of the cow increases. Because of this there have been suggestions that the quantity of food energy allowed for each gallon of milk should be allocated according to a sliding scale which increases with yield. While an allowance of 2.6 lb starch equivalent per gallon might be adequate for lower-yielding cows, an allowance of as much as 3.2 lb starch equivalent per gallon might be needed by cows producing 5 gallons per day. Some evidence supporting this view is given in Fig. 15.5, which shows that, as the allowance of starch equivalent per gallon is increased above 2.6 lb, the response is small with low-yielding cows but rises as the yield increases.

Although a sliding scale may be desirable, it is less easy to apply in practice. The figures in Appendix Table 7 are based on the statistically derived figure of 2.9 lb starch equivalent per 10 lb of 4 per cent. fat milk. Those for milk of other fat contents have been calculated on the basis of their calculated calorific values.

Protein Requirements

The protein requirements for milk production may be estimated by methods analogous to those used for energy requirements

Factorial procedure The protein requirement for the production of milk may be calculated from a knowledge of the protein content together with a measure of the efficiency of utilisation of the protein ingested. Such a measure is given by the biological value (BV). Published work suggests that the biological values of proteins given to ruminants are remarkably constant compared with those obtained with the same proteins for simple-stomached animals. This is due to the degradative and synthetic activities of the microbial population of the rumen, as a result of which the protein presented for digestion by the host is largely microbial in origin. The biological value of such protein is about 80, but for practical purposes a biological value of 70 may be assumed for protein given to lactating cows. For a 4 per cent

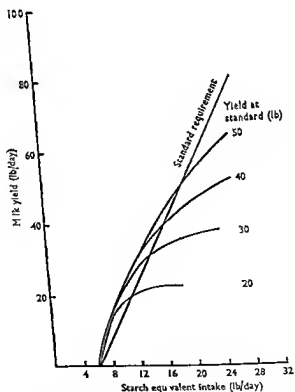


FIG 15.5 Effect of feeding energy levels in excess of standard requirements on milk yield of cows with different lactation yields (From K. L. Blaxter 1962, *The Energy Metabolism of Ruminants*, p 173 Hutchinson, London)

fat milk having 3.4 per cent of crude protein, the digestible crude protein requirement will be

$$0.034 \times 100/70 = 0.049 \text{ lb per lb milk}$$

No account is taken in such a calculation of the increased loss of metabolic faecal nitrogen resulting from the increased food intake necessary for milk production, which is not practicable unless combined requirements for maintenance and lactation are calculated. This may be done by using the equation

$$R = 6.25\{100/B(M \times D + E + G) - M \times D\}$$

as on p. 240, except that G represents the nitrogen in the milk being produced. If the requirements for maintenance and production at different levels of milk production are calculated, then the requirement for the production of a given quantity of milk may be obtained by difference. Such calculations give a slightly increased requirement of 0.051 lb digestible crude protein per pound of milk. Available data on the variation of factorial estimates indicate that this figure should be increased by a 10 per cent safety margin, giving an allowance of 0.056 lb of digestible crude protein per pound.

The standards given in Appendix Table 7 are based on this value.

Feeding trials In these, diets are used which are accepted as satisfactory in all respects other than protein, and the minimum intake of protein adequate for maximum production is determined. Such experiments have to be of a long term nature, since even on deficient diets production may be maintained owing to the cow's ability to utilise her body tissues. This will result in a negative nitrogen balance, and studies of nitrogen balance are often carried out to supplement the main feeding trial. In treating the results of feeding trials, an allowance is made for protein required for maintenance, and the residue equated to milk production. Estimates of digestible protein requirement based on such trials have varied from $1\frac{1}{2}$ times that present in milk to as little as $1\frac{1}{4}$ times in the more recent work. These low levels only apply where the level of crude protein in the diet is of the order of 16 per cent, where the level is reduced to about 12 per cent crude protein, the requirement for milk production rises.

Mineral Requirements

Milk contains about 0.54 g calcium and 0.45 g phosphorus per pound. The amounts are remarkably constant, being under hormonal control and therefore not affected by factors such as dietary level,

they represent the net requirements for the two elements for the production of one pound of milk. Metabolism studies indicate that the feeding of 1 g of calcium and 0.7 g of phosphorus per pound of milk in addition to maintenance requirements is adequate for milk production, which would imply an efficiency of utilisation of dietary calcium for milk production of 54 per cent and of phosphorus of 64 per cent. There are numerous cases where lower allowances have been used over long periods with no ill effects. Thus 25 to 28 g of calcium and 25 g of phosphorus per day have proved adequate for cows producing 10,000 lb of milk per annum over four lactations, which implies a dietary requirement of 0.5 to 0.6 g calcium and 0.5 g phosphorus per pound of milk. Values as low as 0.36 g calcium per pound of milk have been claimed not to cause any ill effects over a period of three lactations. The requirements given in Appendix Table 7 have been derived by factorial calculation and are probably slightly higher than the minimum requirement, but are considered necessary to ensure a normal life span and satisfactory reproduction.

Balance experiments have shown that even very liberal allowances of calcium and phosphorus are frequently inadequate to meet the needs of the cow for these elements during the early part of the lactation, whereas in the later stages and in the dry period storage of calcium and phosphorus takes place. Fig 15.6, for example, shows the cumulative weekly calcium and phosphorus balances throughout a forty-seven week lactation for a mature Ayrshire cow producing 11,254 lb of milk. Despite the negative balances which occurred over considerable periods early in lactation, there was a net positive balance over the lactation and dry period as a whole. It has therefore become normal practice to consider the complete lactation in assessing calcium and phosphorus requirements, early negative balances are regarded as normal, since no ill effects are evident as long as subsequent replenishment of body reserves takes place, and daily requirements for calcium and phosphorus are recommended on the basis of total production over the lactation. It has been suggested that 45 g of calcium and 60 g of phosphorus per day are adequate for a cow yielding 11,000 lb of milk over the lactation, other workers consider that 39 g of calcium and 33 g phosphorus are sufficient for similar yields. Nevertheless, though the lactation approach is satisfactory in many cases, considerable trouble may arise if the allowances used are too low. Where shortage is serious, progressive weakening and breaking of the bones may result, and in less severe cases a premature drying off, which reduces yield and shortens the productive life of the cow. There

seems to be little reason why calcium and phosphorus requirements should not be based on daily or weekly yield measurements. Negative balances in early lactation will thus be reduced and the dangers of undernutrition lessened.

Dietary deficiencies of phosphorus have a greater effect than those of calcium, since for calcium there is a considerable bone reserve which can be mobilised. Phosphorus cannot be mobilised from this source,

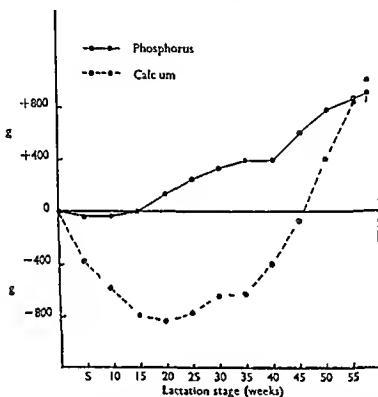


FIG 15.6 Cumulative balances of calcium and phosphorus during lactation (47 weeks) and dry period (From H. B. Ellenberger, J. A. Newlander and C. H. Jones 1931 *Bull. Vt. agric. Exp. Sta.* No. 331.)

and the bone reserves are therefore useless unless dietary calcium is deficient as well as dietary phosphorus. Apart from this source, the animal is entirely dependent on the food for its supply of phosphorus.

Lactating cows are usually given a sodium chloride supplement. This is done by adding the salt to the food or by allowing continuous access to salt licks. The primary need is for sodium rather than chloride, which is more plentiful in normal diets. A deficiency manifests itself in a loss of appetite, rough coat, listlessness, loss of weight and a drop in milk production. Salt hunger and low levels of sodium in plasma and urine may occur in high yielding cows after as little as

three weeks if diets are unsupplemented with sodium chloride. Normally, loss of appetite, weight and production may take about a year to appear. The net requirement for sodium is about 0.27 g per lb of milk or about 0.7 g of sodium chloride. It is usually recommended either that 28 g of sodium chloride per day should be provided in addition to that present in the food, or that 1.5 per cent of sodium chloride should be added to the concentrate ration.

Vitamin Requirements

Vitamins are required by the lactating animal to allow the proper functioning of the physiological process of milk production, and also as constituents of the milk itself. It has yet to be shown that there is a requirement of vitamins specifically for lactation, although they probably have a role in the synthesis of milk constituents, as for instance biotin has in the synthesis of the fat. Most of the evidence points to the conclusion that, provided levels of vitamins in the diet are sufficient for maintenance, normal growth and reproduction, then no further allowance for lactation need be made. But normal levels of vitamins in the milk must be maintained, and sufficient amounts must be given to allow for this. The B-vitamins are an exception, since an adequate supply becomes available as a result of microbial synthesis in the rumen. Maintenance of normal vitamin levels in milk is particularly important where milk is the sole source of vitamins for the young animal, as for example with the young pig.

Milk has a vitamin A potency of about 800 I.U. per lb. Apart from the almost colourless vitamin A, milk contains variable amounts of the precursor β -carotene. This is a red pigment, yellow in dilute solution, as in milk, to which it imparts a rich creamy colour. The vitamin A potency of milk varies widely, being particularly sensitive to changes in dietary levels even though only about 3 per cent of the intake finds its way into the milk. Thus green foods are excellent sources of the provitamin, as is shown by the deep yellow colour and the high potency of the milk produced by grazing cows. Feeding with vitamin A concentrates in excess of levels adequate for reproduction may increase the potency by up to twenty times, but has no effect on the yield or the gross composition of milk. Considerable storage of vitamin A may occur in the body, and these reserves may be tapped to maintain levels in the milk. Since the newborn animal has no vitamin A reserves it is entirely dependent upon milk for its supply, and it is essential to feed the mother during pregnancy and lactation so as to maintain levels in the milk. No problem arises with cattle and sheep which are given

early access to green food, but great care is required with pigs, whose young are entirely dependent upon milk for a longer period.

When lactating dairy cows are kept on diets deficient in vitamin D, and irradiation is prevented, deficiency symptoms appear, showing that the vitamin is essential for normal health. There is no evidence however to show a requirement greater than that which supports maintenance and reproduction. The vitamin D potency of milk is largely influenced by the extent of exposure to sunlight. Large intakes are necessary for small increases in the level in milk. Vitamin D has little effect on the negative balances of calcium and phosphorus during early lactation, but very heavy feeding (with 30,000,000 I.U./day) for three to seven days *pre partum* and one day *post partum* has been claimed to control milk fever (see p. 77).

Dietary intakes of the B-vitamins are of no significance in ruminant animals because of ruminal synthesis. It is probable, however, that a physiological requirement exists for many of them as part of the complicated enzyme systems involved in milk synthesis, and for maintaining normal levels in the milk.

The Effect of Limitation of Food Intake on Milk Production

There is a great deal of evidence to show that reduction of food intake has a profound effect upon both the yield and the composition of milk.

Where cows are kept without food, the yield drops to very low levels of about a pound per milking within three days. At the same time the solids-not-fat and fat contents rise to about twice their previous percentages, this increase being a concentration effect resulting from the reduced yield. Less severe limitation, to about half the production intake indicated by standards of 2.6 lb SE and 0.52 lb PE per gallon of 4 per cent. fat milk, again reduces yield; the percentage of solids-not-fat is lowered but that of the fat is variable (Fig. 15.7).

Limitation of the energy part of the diet has a greater effect than protein limitation on the solids-not-fat content of milk, although it is the protein fraction of the solids-not-fat which is reduced in both cases. Thus a 25 per cent. cut in energy intake had a greater effect than a 40 per cent. cut in protein intake when compared with a diet based on the standards given above (Table 15.13). The fat content of the milk was unaffected by the dietary changes.

Throughout the winter feeding period in the United Kingdom there is a decline in milk yield and in solids-not-fat and fat content in most herds, the rate of decline being most marked during the last two months

of the period. Recent work has indicated that feeding at a higher level than is required by the Woodman standards can prevent this decline from taking place. The traditional pattern is for both yield and solids-not-fat content to increase when cows which have been on winter diets are fed on young spring grass. Where the higher levels of winter feeding have been used, these increases in spring do not take place, which indicates that the standards normally used are not adequate. The position is well illustrated in Table 15.14.

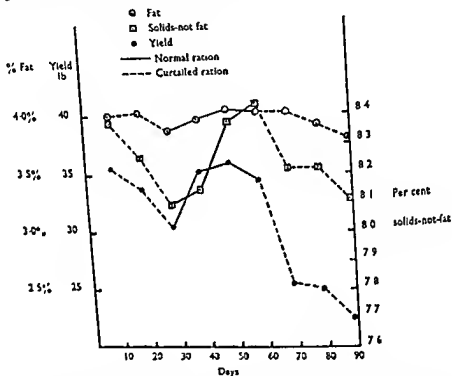


FIG. 15.7. Effect of curtailing nutrient intake to half the required level, on milk composition and yield. (After W. Riddet *et al.* 1941. *N.Z. J. Sci. Technol.* 23A, 80)

TABLE 15.13. Effect of Reduced Levels of Energy and Protein Intake on the Percentage Composition of Milk
(After S. J. Rowland, 1946, *Dairy Industries*, 11, 9)

Diet	Solids-not-fat	Protein	Lactose
Normal *	8.68	3.07	4.71
60 per cent. of normal protein	8.50	2.95	4.65
75 per cent. of normal energy	8.34	2.86	4.61

* 6.0 lb SE and 0.6 lb PE for maintenance of a 1000-lb cow per day + 2.6 lb SE and 0.52 lb PE per 10 lb of 4 per cent. fat milk.

Concurrent with the change to pasture feeding in spring is a fall in the fat content of the milk. Spring pastures have a low content of crude fibre and a high content of soluble carbohydrates; other diets having similar characteristics also bring about a decline in milk fat. The effect of reducing fibre intake and of fine grinding of the fibre is shown in Table 15.15.

TABLE 15.14. Effect of Plane of Nutrition in Late Winter on Changes in Yield and Solids-not-fat after 18 Days on Spring Grass
(After J. A. F. Rook *et al.*, 1960, *J. Dairy Res.*, 27, 427)

<i>Late winter diet</i>	<i>Change in percentage of solids-not-fat</i>	<i>Change in yield (lb)</i>
Control *	+0.11	+2.13
75 per cent. of control	+0.33	+7.70
130 per cent. of control	-0.12	-0.68

* Based on an allowance of 7 lb SE for maintenance of an 11-cwt cow per day + 2.5 lb SE/gal milk.

The effect of low-roughage diets, or of diets where the hay is ground, is accentuated by a high soluble carbohydrate content, as in pasture herbage. Increasing the solubility of maize carbohydrate in the diet lowers the fat content of the milk produced, and this is associated with a fall in the proportion of acetic acid in the rumen volatile fatty acids (Table 15.16).

TABLE 15.15. Comparison of Fat Contents of Milks produced on various Diets with that of Milk produced on a Diet containing 12 lb of Hay+Concentrates
(After C. C. Balch *et al.*, 1954, *J. Dairy Res.*, 21, 172)

<i>Diet</i>	<i>Change in percentage of milk fat</i>
8 lb hay+concentrates	-1.16
8 lb ground hay+concentrates	-1.72
4 lb hay+concentrates	-1.12

The fall in fat content in such cases is due to a net reduction in milk fat synthesis, for which acetate is the main precursor. The achievement of the ideal type of rumen fermentation, yielding the right mixture of volatile fatty acids for milk production, demands a nice balance between roughage and concentrate in the diet. A certain minimum of roughage in the long state is essential to maintain fat content, and it must be enough to ensure a level of 7.5 to 8 per cent. of crude

fibre in the dry matter of the diet. On the other hand if the crude fibre content exceeds about 16 per cent of the dietary dry matter, then the efficiency of milk production falls and this will be reflected in lower yields.

There is a tendency for dietary fat to be regarded simply as a source of energy. However when rats, young pigs and young ruminants are given diets adequate in energy but are deprived of fat, they fail to grow, develop dermatitis and eventually die. The necessity for dietary fat arises from the fact that it supplies the animal with the essential fatty acids (p. 23). No studies of the needs of adult farm animals for essential fatty acids seem to have been made, probably because natural foods contain adequate amounts and their provision is not a problem in practice. It has been shown, however, that when fat

TABLE 15.16 Relation of Dietary Cooked Starch to Milk Fat Content and to Rumen Volatile Fatty Acids
(After W. L. Ensor *et al.*, 1959 *J. Dairy Sci.* 42, 189)

Diet	Percentage change in fat content	Molar percentage of total rumen volatile fatty acids	
		Acetic acid	Propionic acid
28-32 lb ground and pelleted hay	0	67.9	20.2
28 lb ground and pelleted hay + 4 lb ground maize	-13	61.9	25.1
28 lb ground and pelleted hay + 4 lb cooked maize	-53	53.9	31.1

is replaced by an isocaloric amount of starch in the diet of the lactating cow then milk yields may be lowered, and there is also some evidence that diets having 5 to 7 per cent of ether extract produce more milk than diets containing less than 4 per cent. Nevertheless care must be taken that certain highly unsaturated fats are not given to excess, or milk fat content may be reduced. Cod liver oil at levels of 6 to 8 oz per day can reduce fat content by as much as 25 per cent, and herring oil has a similar effect. Levels of up to 12 per cent of fat in the diet have been given to dairy cows without ill effects but here the fat was highly saturated and was of mammalian origin. The level of fat which may be safely included in the diet of the lactating cow is important in view of its high energy value which makes it convenient for inclusion in high energy dairy cakes.

NUTRIENT REQUIREMENTS OF THE LACTATING DAIRY GOAT

In addition to the dairy cow, the goat is also used in the United Kingdom for the commercial production of milk for human consumption. Yield varies with breed (see Table 15.17) and with stage of lactation, the peak yield occurring at about four weeks. A lactation normally lasts for about eight to nine months, during which time up to 3000 lb of milk may be produced. Breed and stage of lactation affect also the composition of the milk. Total solids content falls to a minimum value at about four months, rises for the succeeding three months and then remains constant until the close of the lactation.

TABLE 15.17. Yield and Composition of Milk for various Breeds of Goats
(After F. Knowles and J. E. Watkin, 1938, *J. Dairy Res.*, 9, 153)

Breed	Fat (per cent.)	Crude protein (per cent.)	Calcium (per cent.)	Phosphorus (per cent.)	Lactation yield (lb)
Anglo-Nubian	5.6	3.85	0.156	0.139	1846
British Saanen	4.1	3.10	0.126	0.104	2917
British Alpine	4.3	3.27	0.137	0.118	2500
British Toggenburg	4.5	3.41	0.144	0.126	2393

As with the milk of the dairy cow, the energy content of goat's milk may be calculated from the fat content. The equation * is

$$y = 39.618 + 9.564x,$$

where y = kcal/100 ml and x = percentage of fat.

A milk with 4 per cent. fat would then have a calorific value of 354 kcal/lb. The efficiency of utilisation of metabolisable energy for lactation is probably very similar to that for the cow, i.e. about 70 per cent., which means that 506 kcal metabolisable energy or 0.28 lb starch equivalent is required to produce one pound of milk. Such a milk would contain about 3.3 per cent. protein, 0.13 per cent. calcium and 0.11 per cent. phosphorus. From a comparison with standards used for the dairy cow, requirements based on these figures may be calculated to be 0.052 lb digestible crude protein, 0.9 g calcium and 0.7 g phosphorus per pound of milk. In addition the lactating goat requires 0.6 g sodium chloride per pound of milk produced.

NUTRIENT REQUIREMENTS OF THE LACTATING EWE

The lactation of the ewe usually lasts from twelve to twenty weeks, although individuals show very considerable variations. Stage of

* From W. E. Petersen and C. W. Turner, 1939, *J. Nutr.*, 17, 293.

lactation has a pronounced effect on milk yield, which is at a maximum at the second to third week and then falls steadily, as shown for Suffolk ewes in Fig 15 8

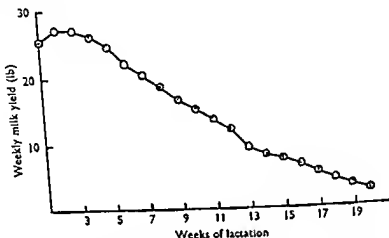


FIG 15 8 Effect of stage of lactation on milk yield of the ewe
(From L. R. Wallace 1948 *J agric Sci* 38, 93)

Effect of stage of lactation on milk yield of the ewe It has been calculated that about 38 per cent of the total yield is obtained in the first four weeks of lactation, 30 per cent in the succeeding four weeks, 21 per cent in the next four weeks and 11 per cent in the final four weeks. Comparison of the milk yields of different breeds is difficult,

TABLE 15 18 Lactation Yields of different Breeds of Sheep

Breed	Duration of lactation (weeks)	Lactation yield (lb)
Suffolk	20	294
Border Leicester × Cheviot	16	366
Romney	12	267
Cheviot	13	205
Blackface	8	192
Merino	12	144

since the data have been obtained under widely differing climatic conditions, levels of feeding and sampling techniques. They indicate, however, that breed differences do exist (see Table 15 18), and that within breed differences are frequently large.

Animals suckling more than one lamb produce more milk than those suckling single lambs. The figures may be as far apart as 240 and 352

pounds respectively for lactation yields for Suffolk ewes with single and twin lambs, and 307 and 514 pounds for Border Leicester-Cheviot ewes. The higher yield is probably due to higher frequency of suckling and greater emptying of the udder, indicating that a single lamb is incapable of removing sufficient milk from the udder to allow the full milking potential of the ewe to be fulfilled.

Data on the composition of the milk of the ewe are very scarce. Such factors as sampling techniques, stage of lactation and milking intervals all affect composition and figures are not strictly comparable. The effect of breed is shown in Table 15.19.

TABLE 15.19. Effect of Breed on the Percentage Composition of Ewe's Milk
(After R. E. Neidig and E. J. Iddings, 1919, *J. agric. Res.*, 17, 19)

<i>Breed</i>	<i>Fat</i>	<i>Solids-not-fat</i>
Hampshire	7.1	9.75
Cotswold	7.7	9.52
Shropshire	8.1	9.67
Southdown	7.5	10.36

The average composition of ewe's milk is given in Table 15.6, and a calorific value of about 550 kcal/lb may be calculated. By analogy with the dairy cow the efficiency of utilisation of metabolisable energy for lactation in the ewe may be taken as about 70 per cent., so that the metabolisable energy requirement per pound of milk produced is

$$550 \times 100/70 = 786 \text{ kcal of metabolisable energy.}$$

From the average figures for crude protein, calcium and phosphorus and by using the same approach as for the dairy cow, the requirements per pound of milk produced may be calculated to be 0.09 lb of digestible crude protein, 2.0 g of calcium and 1.2 g of phosphorus. In rationing the ewe an assumption of yield has to be made. In *Rations for Livestock* the figure used is 3 gallons per week or about 4½ lb per day, but this takes no account of the variation during lactation which is shown in Fig. 15.8. From this point of view the approach of the National Research Council is preferable: if we assume a yield of 4½ lb per day for the first eight to ten weeks, and 50 per cent. of this value thereafter. A lactating ewe would then require 3537 kcal metabolisable energy (1.9 lb SE), 0.41 lb DCP, 9.0 g calcium and 5.5 g phosphorus per day, in addition to its maintenance ration, during the first ten weeks of lactation; the addition of half of these quantities to a maintenance ration should suffice thereafter. The figures given in Appendix Table 9 are so derived.

NUTRIENT REQUIREMENTS OF THE LACTATING SOW

A lactation normally lasts for about eight weeks in the sow. The maximum yield occurs at about three weeks, the production then remains relatively constant from the third to the fifth week, and

TABLE 15 20 Variation in Milk Yield of the Sow with Stage of Lactation
(From G A Lodge 1962, *The nutrition of the lactating sow* In *Nutrition of Pigs and Poultry*, ed by J T Morgan and D Lewis Butterworth London)

	Week of lactation								Mean
	1	2	3	4	5	6	7	8	
Percentage variation from the mean	82	107	115	115	115	107	87	76	100
Mean daily yield (lb) based on 14 lb mean	11.5	15	16	16	16	15	12	10.5	14

declines thereafter. Yield varies also with breed, age and litter size, increasing with the number of piglets suckled although the yield per piglet declines (see Tables 15 20 and 15 21). Estimates of daily milk yield in the sow vary considerably, but the mean figure of 14 lb quoted in the tables is widely accepted.

After the first week, which is a colostral period, the total solids content of the milk remains constant. The fat content falls from the third week, while the solids not fat rises owing to an increase in protein content.

TABLE 15 21 Variation in Milk Yield of the Sow with Variation in Litter Size
(From G A Lodge 1962 *The nutrition of the lactating sow* In *Nutrition of Pigs and Poultry* ed by J T Morgan and D Lewis Butterworth London)

	Litter size										
	3	4	5	6	7	8	9	10	11	12	
Mean daily recorded yield (lb) *	7.5	—	11.6	13.6	15.6	17.8	18.8	19.5	19.9	20.3	
Mean daily yield (lb) based on 14 lb for a litter of 8	5.9	7.7	9.2	10.7	12.3	14.0	14.9	15.5	15.8	16.0	

* Data of S. Berge and T. Indrebø 1953 *Meld. Norg. Landbr. Høisk.* 33, 389

Energy Requirements

The net requirements for energy for the lactating sow are the sum of the energy expended in maintenance and the gross energy of the milk produced. For a 450-lb sow the basal metabolism may be calculated to be 4265 kcal, and if we allow 30 per cent of the basal metabolism for activity we obtain a maintenance requirement of 5545 kcal. The need for digestible energy to satisfy this requirement is

$$5545 \times 100/75 = 7393 \text{ kcal}$$

when the efficiency of utilisation of digestible energy for maintenance is 75 per cent

The requirement for milk production may be calculated as follows. Assume a litter of 8 piglets and a daily milk production of 14 lb. The gross energy of the milk, calculated from data in Table 15.6, is 591 kcal/lb, giving an energy content of the milk secreted daily of 8274 kcal. The net utilisation of digestible energy for lactation is about 70 per cent. The digestible energy requirement for lactation is then

$$11,820 + 7393 = 19,213 \text{ kcal/day}$$

A typical pig meal might have a digestible energy content of 1300 kcal/lb, and the meal requirement of the sow would then be about 14½ lb per day. In terms of the meal suggested in Appendix Table 10 the requirement would be about 13 lb per day.

The validity of the results of such factorial calculations depends in turn upon the validity of the assumptions upon which the calculations are based. The critical assumptions in this case are the yield of milk, and that the maintenance requirement of the lactating sow is the same as that of a non lactating sow. There is evidence that the maintenance requirement is in fact considerably greater, and it has been suggested that, instead of treating maintenance and lactation separately, a gross efficiency of energy conversion for lactation should be used in calculating energy requirements. The gross efficiency is the energy value of the milk as a percentage of the digestible energy of the feed, and is considered to be about 45 per cent. Assuming a gross energy value of 1.25 kcal/g for milk, and allowing for the differences in yield with lactation stage and litter size shown in Tables 15.20 and 15.21, the energy requirements for sows with different sizes of litter at different stages of lactation have been calculated. These requirements, in terms of a meal having 1300 kcal digestible energy per lb, are given in Table 15.22.

These and the previously derived factorial requirement values are considerably above the commonly used United Kingdom allowances of 2 lb of meal for the sow and 1 lb per piglet, i.e. 10 lb of meal for a sow with 8 piglets

In present day conditions it is normal for a sow to gain weight during pregnancy and to lose it in the early part of the following lactation. During pregnancy food is being used to build up reserves which are subsequently mobilised to provide the raw material for lactation. This process occurs even where high levels of food are made

TABLE 15 22. Estimated Daily Meal Requirement (lb) of the Lactating Sow *
(From G. A. Lodge 1962, *The nutrition of the lactating sow* In *Nutrition of Pigs and Poultry*, ed. by J. T. Morgan and D. Lewis, Butterworth, London)

Litter size	Week of lactation								Mean
	1	2	3	4	5	6	7	8	
3	4.8	6.3	6.7	6.7	6.7	6.3	5.0	4.4	5.9
4	6.3	8.2	8.8	8.8	8.8	8.2	6.6	5.8	7.7
5	7.5	9.8	10.5	10.5	10.5	9.8	7.9	6.9	9.2
6	8.8	11.4	12.2	12.2	12.2	11.4	9.2	8.0	10.7
7	10.1	13.2	14.0	14.0	14.0	13.2	10.6	9.2	12.3
8	11.5	15.0	16.0	16.0	16.0	15.0	12.0	10.5	14.0
9	12.2	15.9	17.0	17.0	17.0	15.9	12.8	11.2	14.9
10	12.7	16.6	17.7	17.7	17.7	16.6	13.3	11.6	15.5
11	13.0	16.9	18.0	18.0	18.0	16.9	13.6	11.9	15.8
12	13.1	17.1	18.2	18.2	18.2	17.1	13.8	12.0	16.0

* Meal with a digestible energy value of 1300 kcal/lb

available to the lactating sow, and it has been suggested that the provision of such levels is only economic where gain in weight during pregnancy is limited to that arising from the laying down of the products of conception, the raw material and energy for milk production must eventually come from the food, and it is suggested that this will be done more efficiently by direct provision of food during lactation than by using the pregnant animal as an intermediary. A true gain in sow body weight of 15–20 lb gives better reproductive performance, and a certain amount of laying down of reserves destined to be used up in the subsequent lactation is acceptable. Where higher feeding levels such as those given in Table 15 22 are used, it has been found that sows lose less weight and produce more milk than animals fed conventionally. On the other hand the piglets reared on sows receiving the high intakes showed no significant advantage. This was partly because the lower-yielding sows produced richer milk, and partly because the increased

yields were obtained after the third week when creep feed was being eaten, and the piglets on the low-yielding sows ate more of this than the others. Consumption of creep feed, however, is variable and cannot always be relied upon to make good deficiencies in the milk yield of the sow; for safety it would therefore be preferable to feed the piglets via the milk rather than by the more efficient direct creep feeding.

Protein Requirements

The net protein requirement for a lactating animal is made up of that required for maintenance *plus* that secreted in the milk. As with the maintenance requirement for energy, estimates of protein requirements

TABLE 15.23. Amino Acids Requirements of Sows for Milk Production

<i>Amino acid</i>	<i>Per cent. of milk *</i>	<i>Requirement (g/lb of milk) †</i>
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acids calculated from them. The estimates are based on an assumed digestibility of 80 per cent and an assumed biological value of 70

Mineral Requirements

There is no evidence to suggest that any minerals other than calcium and phosphorus have to be provided in the diet of lactating sows at levels above those necessary for maintenance and normal reproduction. Balance experiments indicate that the gross efficiency of utilisation of calcium and phosphorus for lactation is about 50 per cent. Table 15.6 shows that the milk of the sow contains 0.25 per cent of calcium and 0.17 per cent of phosphorus. A sow producing 14 lb of milk per day would thus be secreting 16 g of calcium and 11 g of phosphorus. The dietary requirement to enable this to be maintained would be 32 g calcium and 22 g phosphorus. In a meal given at 14 lb per day this would require 0.5 per cent calcium and 0.35 per cent of phosphorus. The requirements given in Appendix Table 10 include margins of safety of 10 to 15 per cent.

Vitamin Requirements

Little information is available concerning the vitamin requirements for lactation of the sow. Those given in Appendix Table 10 are the same as for the pregnant sow. The assumption is made that levels which allow normal reproduction and maintenance are adequate for lactation.

FURTHER READING

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GRASS AND FORAGE CROPS

PASTURE

The natural food of herbivorous domestic animals is pasture herbage, and for a large part of the year this food forms all or most of the diet. Grasslands may be divided into two main groups, *natural grassland*, which includes rough and hill grazing, and *cultivated grassland*, which may be further subdivided into permanent and temporary pastures. The latter form part of a rotation of crops, whereas permanent pasture is intended to remain as grass indefinitely. Natural grasslands normally include a large number of species of grasses, legumes and herbs, whereas cultivated grasslands may consist of pure species or mixtures of relatively small numbers of species.

Chemical Composition

The composition of pasture dry matter is very variable, for example, the crude protein content may range from as little as 3 per cent in very mature herbage to over 30 per cent in young heavily-fertilised grass. The crude fibre content is broadly related inversely to the crude protein content, and may range from 20 per cent to as much as 40 per cent in very mature samples.

The moisture content of pasture is of particular importance where a crop is being harvested for conservation, and is high in the early stages of growth, usually between 75 per cent and 85 per cent, and falls as the plants mature to about 65 per cent. In addition to stage of growth, weather conditions greatly influence the moisture content.

The soluble carbohydrates of grasses include fructosans and the sugars glucose, fructose, sucrose, raffinose and stachyose (see Table 16.1). Their total percentage is very variable, ranging in the dry matter from as little as 4 per cent in some cocksfoot varieties to over 30 per cent in certain varieties of Italian ryegrass.

The cellulose content is generally within the range of 20-30 per cent, while hemicelluloses may vary from 10 to 30 per cent of the dry matter. Both these polysaccharide components increase with maturity, so

also does the lignin, which influences adversely the digestibility of the useful nutrients except the soluble carbohydrates, which are completely digestible

Proteins are the main nitrogenous compounds in herbage, and although the total protein content decreases with maturity the relative proportions of amino acids do not alter greatly. Grass proteins are particularly rich in the amino acid, arginine, and also contain appreciable amounts of glutamic acid and lysine. The non-protein nitrogenous (NPN) fraction of herbage varies with the physiological state of the plant. Generally, the more favourable the growth conditions, the higher is the NPN content as well as the total nitrogen value, and as the plants

TABLE 16.1 Percentage Composition of the Dry Matter of a Sample of Italian Ryegrass cut at a Young Leafy Stage

Proximate composition		Carbohydrates		Nitrogenous components		Other constituents
Crude protein	18.7	Glucose	2.2	Total N	3.0	Lignin 8.3
Ether extract	3.5	Fructose	1.9	Protein N	2.7	
Crude fibre	23.6	Sucrose	3.5	Non protein N	0.3	
Nitrogen free extractives	44.1	*Oligosaccharides	2.0			
Ash	10.2	Fructosans	5.6			
		Galactan	1.1			
		Araban	3.0			
		Xylan	11.8			
		Cellulose	26.2			

* Excluding sucrose

mature both total N and NPN contents decrease. The main components of the NPN fraction are amino acids, and amides such as glutamine and asparagine, which are concerned in protein synthesis, nitrates may also be present, and considerable attention has recently been given to the presence of these in pasture herbage because of their toxic effects on farm animals. It has been reported that toxic symptoms may occur in animals grazing herbage containing more than 0.07 per cent nitrate nitrogen in the dry matter (equivalent to 0.5 per cent potassium nitrate), while amounts greater than 0.22 per cent may be lethal. In feeding trials, however, concentrations considerably above these levels have been tolerated. Nitrate is converted into nitrite in the digestive tract and when absorbed results in the formation of methaemoglobin (oxidised haemoglobin), toxic symptoms include trembling, staggering, rapid respiration and death. The nitrate content of grasses varies with species, variety and manuring, although the amount present is generally directly related to the crude protein content.

The lipid content of pasture, as determined in the ether extract fraction, is comparatively low and rarely exceeds 4 per cent. of the dry matter. Oils extracted from grass and forage crops have been shown to be rich in unsaturated fatty acids.

The mineral content of pasture is very variable, depending upon the species, soil type and fertiliser application; an indication of the normal range in content of some essential elements is given in Table 16.2.

TABLE 16.2. Ranges of Essential Element Contents of Pasture Grass*

<i>Element</i>	<i>Low</i>	<i>Normal</i>	<i>High</i>
		(percentage of dry matter)	
Potassium	<1.0	1.2 —2.8	>3.0
Calcium	<0.3	0.4 —0.8	>1.0
Magnesium	<0.1	0.12—0.26	>0.3
Phosphorus	<0.2	0.2 —0.35	>0.4
		(ppm of dry matter)	
Iron	<45	50—100	>200
Manganese	<30	40—200	>250
Copper	<3	4—8	>10
Zinc	<15	20—80	>100
Cobalt	<0.08	0.08—0.25	>0.30
Molybdenum	<0.4	0.50—3.0	>5

* Legumes generally contain rather higher levels of calcium, magnesium, copper and cobalt, so that mixed herbage containing clover tend to be richer in these elements.

Green herbage is an exceptionally rich source of carotene, the precursor of vitamin A, and quantities as high as 550 ppm may be present in the dry matter of young green crops. Herbage of this type supplies about 100 times the requirement of a grazing cow when eaten in normal quantities.

It has generally been considered that growing plants do not contain vitamin D, although precursors are usually present. Recent studies suggest, however, that vitamin D may be present in herbage but in relatively small amounts. The increased vitamin D content of mature herbage compared with young material may be due in part to the presence of dead leaves in which vitamin D₂ has been produced from irradiated ergosterol.

Most green forage crops are good sources of vitamin E and of many of the B-vitamins, especially riboflavin.

Factors Influencing the Nutritive Value of Pasture

Species. The agricultural value of any particular species in a grassland sward depends upon many factors other than the nutritive value.

The persistence and productivity of a species or variety are of great economic importance, and the selection of a seeds mixture for sowing as a temporary pasture will also depend on whether the herbage is required for hay, silage, or predominantly for grazing

The agricultural value of grasses such as perennial ryegrass (*Lolium perenne*), Italian ryegrass (*Lolium multiflorum*), cocksfoot (*Dactylis glomerata*), timothy (*Phleum pratense*) and meadow fescue (*Festuca pratensis*) is high, and these species form the basis of seeds mixtures for temporary pastures. On the other hand grasses such as Yorkshire fog (*Holcus lanatus*) and the bents (*Agrostis* spp.) are regarded as inferior grasses. This classification of species may be misleading as regards nutritive value since most grasses in the early stages of growth have a relatively high feeding value, but the poorer quality of the inferior grasses is more marked with the advancing season. Among the better grasses, differences in composition and digestibility exist between species and even varieties.

It is frequently assumed that different grasses at the same morphological stage have the same digestibility. Recently it has been shown that this is not always so, and experiments in which S₃₇ cocksfoot has been compared with S₂₃ and S₂₄ ryegrasses suggest that, although the ryegrasses are similar in organic matter digestibility when cut at the same stages of growth, the digestibility of the organic matter in the cocksfoot at the same growth stage is lower by about 6 percentage units.

Variations in carbohydrate content occur between species, for example, cocksfoot is generally of lower soluble carbohydrate content than the ryegrasses, although considerable varietal differences in any one species have been reported. With soluble carbohydrates seasonal and environmental effects are probably of major importance.

Although the species of grasses mentioned so far are the most important in temporary pastures, there are a number of moorland species which provide valuable grazing on hill and marginal land. The moorland grasses in these permanent pastures include sheep's fescue (*Festuca ovina*) the common and brown bents (*Agrostis* spp.), white bent (*Nardus stricta*) and flying bent (*Molinia caerulea*). Many of the moorland grasses are valuable sources of nutrients in the spring and early summer, the mature grasses tend to be more fibrous and of lower digestibility than the more productive species. These moorland grasses can be regarded as 'seasonal foods'.

Clovers are generally richer in protein and minerals, especially calcium, phosphorus, magnesium, copper and cobalt, than the grasses

The commonest clovers which occur in pasture are the white clovers (*Trifolium repens*), and the red clovers (*Trifolium pratense*).

The sugars present in clovers are similar to those in grasses, the main sugar being sucrose. Fructosans are generally absent, but starch, which is not usually present in grasses, may occur in clover, and concentrations of this polysaccharide as high as 5 per cent. have been reported in the dried leaves of red clover.

Herbs such as chicory (*Cichorium intybus*), plantain (*Plantago* spp.), yarrow (*Achillea millefolium*) and burnet (*Poterium sanguisorba*) are sometimes present in pastures and are excellent sources of many of the essential major and trace elements, particularly calcium, phosphorus, magnesium and manganese. Burnet is specially rich in magnesium, and values as high as 1.4 per cent. in the dry matter have been reported.

Stage of growth. Stage of growth is the most important factor influencing the composition and nutritive value of pasture herbage. As plants grow there is a greater need for structural tissues, and therefore the structural carbohydrates (cellulose and hemicelluloses) and lignin increase. This is reflected in the crude fibre content, which in the dry matter may increase from below 20 per cent. in the young plant to as much as 40 per cent. in the mature crop. As the plant ages the percentage of protein decreases; there is therefore a reciprocal relationship between crude protein and crude fibre contents in a given species, although this relationship can be upset by the application of nitrogenous fertilisers.

The variations in chemical composition of timothy at different stages of growth are shown in Table 16.3. In addition to the changes in crude protein and carbohydrates, changes also occur in the mineral or ash constituents. The total ash content decreases as the plant matures. This is reflected in the calcium content, which follows a similar pattern to that of the total ash in grasses. The magnesium content is generally high in the early spring, but falls off sharply; during the summer it rises, reaching high values in the autumn.

The digestibility of the organic matter is one of the main factors determining the nutritive value of forage, and this may be as high as 85 per cent. in young spring pasture grass and as low as 50 per cent. in winter faggage. Although there is a relationship between stage of growth and digestibility in that digestibility decreases as plants mature, the relationship is complicated by there being a spring period of up to a month during which the herbage digestibility remains fairly constant. This period has been described as the 'plateau'. The end of this period is associated in some plant species with ear emergence, after which

digestibility of organic matter may decrease abruptly at the rate of half a unit per day

As well as influencing the amount of nutrients available to the animal, digestibility is an important factor controlling intake. The more digestible the pasture herbage, the more grazing animals will consume (see Chapter 10)

The decrease in digestibility with stage of growth is also reflected in the net energy values, as shown in Table 16.4 for four cuts of S₂₃

TABLE 16.3 Chemical Composition of Established Timothy at Different Stages of Growth

(After R. Waite and K. N. S. Sastry, 1949, *Emp. J. exp. Agric.*, 17, 179)

		Composition of dry matter						
Date		Crude protein (per cent)	True protein (per cent)	Carotene (ppm)	Crude fibre (per cent)	Ether extract (per cent)	Ash (per cent)	Moisture (per cent)
May	20	18.4	16.5	274	20.3	3.54	8.00	77.2
	26	18.8	15.7	273	23.2	3.56	8.50	81.6
June	2	14.2	12.8	156	26.3	3.74	7.15	79.0
	10	10.6	8.8	128	28.7	2.91	7.72	80.6
	16	9.2	8.7	108	30.8	3.02	6.86	76.1
	23	7.1	5.8	74	32.6	2.18	6.50	72.2
	30	6.3	5.5	72	30.4	2.12	5.98	65.5
July	7	6.8	4.4	66	31.2	1.79	6.12	65.2
	14	5.5	3.8	88	32.1	1.64	5.62	65.0

ryegrass. The low net energy value of mature herbage is not only due to a low organic matter digestibility, but is also associated with a high concentration of cellulose. This polysaccharide encourages, in the rumen, high levels of acetic acid, which has a low efficiency of utilisation for the production of depot fat (see Chapter 11).

Soils and fertiliser treatment The type of soil may influence the composition of the pasture, especially its mineral content. Plants normally react to a mineral deficiency in the soil either by limiting their growth or by reducing the concentration of the element in their tissues, or more usually by both.

The acidity of the soil is an important factor which can influence, in particular, the uptake of many trace elements by plants. Both manganese and cobalt are poorly absorbed by plants from calcareous soils, whereas low molybdenum levels of herbage are usually associated with acid soils. Teart, associated with high herbage molybdenum levels, generally occurs on pasture grown on soils derived from Lower Liass clay or limestone.

Liberal dressings of fertilisers can markedly affect the mineral content of plants, and it is also known that the application of nitrogenous fertilisers can increase the crude protein of pasture herbage and influence the amide and nitrate content. Application of nitrogenous fertilisers also depresses the fructosan content of grasses. Fertilisers may also affect, indirectly, the nutritive value of a sward by altering the botanical composition. For example legumes do not thrive on a lime-deficient soil, while heavy dressings of nitrogen encourage growth of grasses and at the same time depress clover growth.

TABLE 16.4 Composition (per cent Dry Matter) and Net Energy Values (kcal/kg Dry Matter) of Four Cuts of S₂₃ Ryegrass
(After D. G. Armstrong, *Proc. 8th Int. Grassl. Congr.* 1960, p. 485)

	<i>Cut 1</i> <i>Young leafy</i>	<i>Cut 2</i> <i>Late leafy</i>	<i>Cut 3</i> <i>Ear emergence</i>	<i>Cut 4</i> <i>Full seed</i>
<i>Proximate composition</i>				
Ash	8.1	8.5	7.8	5.7
Crude protein	18.6	15.3	13.8	9.7
Ether extract	3.8	3.1	3.0	2.5
Crude fibre	21.2	24.8	25.8	31.2
Nitrogen free extractives	48.3	48.3	49.6	50.9
<i>Other constituents</i>				
Crude lignin	3.6	4.6	5.5	7.5
Cellulose	25.3	28.4	29.9	35.6
Soluble carbohydrates	12.5	11.5	11.5	10.1
<i>Net energy values *</i>				
For maintenance	2452	2234	2110	1738
For production	1653	1641	1339	903

* Determined with mature sheep

Other factors affecting the nutritive value of pasture Such factors as climate, season and rate of stocking may influence the nutritive value of pasture. The concentration of sugars and fructosans, for example, can be influenced markedly by the amount of sunshine received by the plant. Generally on a dull cloudy day the soluble carbohydrate content of grass will be lower than on a fine sunny day. Rainfall can affect the mineral composition of pasture herbage. Calcium, for example, tends to accumulate in plants during periods of drought but to be present in smaller concentration when the soil moisture is high; on the other hand phosphorus appears to be present in higher concentrations when the rainfall is high.

Both under grazing and over-grazing can influence the composition

of the pasture With under grazing the plants become mature and of low digestibility, resulting in reduced intake of dry matter Overstocking will tend to eliminate or weaken many of the best grasses by depriving them of the opportunity for building up and storing reserve nutrients in their roots

It is generally considered that autumn grass has not the same nutritive value as spring grass, even when the stage of growth is similar There is evidence that the soluble carbohydrates are frequently low in autumn herbage, which may be partly a seasonal effect and partly a depression caused by application of nitrogen fertiliser A depression in readily available carbohydrate may have a twofold effect Firstly, the rumen fermentation products will be high in acetic acid, which has a relatively low energy value for depot fat formation, and secondly, the herbage may contain insufficient fermentable carbohydrate for the rumen micro organisms to utilise the nitrogenous components efficiently

OTHER FORAGE CROPS

Legumes

Some of the more commonly grazed clovers have already been described under 'Pasture' Lucerne (*Medicago sativa*) is an important legume which is widely grown under both tropical and temperate conditions Unlike grasses, lucerne does not possess large amounts of reserve polysaccharides in the form of fructosans, but it does contain small amounts of starch and relatively large quantities of pectin The protein content is comparatively high, and if the crop is cut in the early flowering stage the crude protein content is likely to be above 20 per cent Under conditions in the United Kingdom lucerne tends to be high in fibre, particularly the stem, which at the flowering stage may contain 50 per cent crude fibre Table 16.5 shows the composition of lucerne at three different stages of growth The relatively low digestibility of the fibre is ascribed to lignification being more rapid in the lucerne plant, with its erect type of growth than in grasses

In common with most green legume crops, lucerne is a valuable source of the element magnesium, and quantities ranging from 0.20 to 0.36 per cent in the dry matter occur

In the U.S.A. lucerne, known there as alfalfa, is used as a pasture crop, although its management for this purpose requires considerable care in order to avoid over grazing

Sainfoin (*Onobrychis sativa*) is a legume of less economic importance than lucerne, and in the United Kingdom is confined to a few main

areas in the south. In common with most green forages the leaf is richer than the stem in crude protein, ether extract and minerals, especially calcium. Changes which occur in the composition of the plant are mainly due to variation in stem composition and leaf-stem ratio. The crude protein content in the dry matter may vary from 24 per cent at the early flowering stage to 14 per cent at full flower. Corresponding crude fibre values at similar stages of growth may be 14 and 27 per cent.

TABLE 16.5 Percentage Composition of the Dry Matter of Lucerne
(After S. J. Watson and M. J. Nash, 1960, *The Conservation of Grass and Forage Crops*, p. 12. Oliver and Boyd, Edinburgh)

	<i>Pre bud</i>	<i>In bud</i>	<i>In flower</i>
Crude fibre	22.1	26.5	29.4
Crude protein	25.3	21.5	18.2
Ash	12.1	9.5	9.8
Digestible crude protein	21.3	17.0	14.1
Starch equivalent	59.8	50.1	44.9
Indigestible crude fibre	8.0	12.8	16.2

Peas, beans and vetches are sometimes grown as green fodder crops, and if cut at the early flowering stage are similar in nutritive value to other legumes.

A trouble which is frequently encountered in cattle and sheep grazing on legume dominant pastures is *bloat*, characterised by an accumulation of gas in the rumen. The primary cause of bloat is the retention of the fermentation gases in a stable foam, preventing their elimination by eructation (see p. 118).

Cereals

Cereals are sometimes grown as green forage crops, either alone or mixed with legumes. Like the grain, the forage is rich in carbohydrate and low in protein, its nutritive value depending mainly on the stage of growth when harvested. The crude protein content of the dry matter at the cereal grazing stage is generally within the range of 8–12 per cent. At the time of ear formation the percentage of crude fibre falls as a result of the great increase in soluble carbohydrates.

Brassicas

The genus *Brassica* comprises some forty species, of which the following are of agricultural importance: kales, cabbages, rapes, turnips and swedes. Some of the brassicas are grown primarily as root crops, and these will be discussed in a later chapter.

Kales There are two main varieties, 'marrow stem' and 'thousand headed', both providing large yields of fodder for winter feeding. The varieties are similar in feeding value and have crude protein contents in the dry matter generally between 14 and 17 per cent. The dry matter content is low, averaging about 15 per cent. Kale, like most brassicas, is liable to contain goitrogens which can cause goitre in animals if given in large amounts (see p. 90). Kales are excellent sources of calcium, of which they may contain up to 2 per cent in the dry matter.

Cabbages Two varieties are grown, the 'drumhead' and the 'open leaved'. The latter is richer in protein and has a higher starch equivalent value than the drumhead variety. The crude fibre content of the dry matter of cabbages is much lower (about 15 per cent) than that of most green forage crops, and consequently the starch equivalent value of the dry matter is relatively high (about 60 for the open leaved variety). Like the kales, cabbages are low in dry matter content, which may be as little as 11 per cent in the drumhead variety, and they are rich in calcium.

Green Tops

Mangold, fodder beet, sugar beet, turnip and swede tops may all be used for feeding farm animals. Care is required in feeding with mangold, fodder and sugar beet tops, since they contain a toxic ingredient which may lead to extensive scouring and distress and in extreme cases death. The risk appears to be reduced by allowing the leaves to wilt. The toxicity has been attributed to oxalic acid and its salts, which are supposed to be reduced or removed by wilting. A recent study casts some doubt on this theory, since the oxalate content of the leaves is practically unaffected by wilting. It is possible that the toxic substances are not oxalates but other factors which are destroyed during wilting.

Swede and turnip tops are safe to feed, and may have a crude protein content in the dry matter as high as 20 per cent, the digestibility of the organic matter being about 70 per cent.

Sugar beet tops generally contain the upper part of the root as well as the green leaves and are more digestible, about 77 per cent. All these green tops are excellent sources of carotene.

Oestrogenic Substances in Forage Crops

More than 50 species of plants are known to contain compounds capable of producing oestrus in immature female animals. Although

the potency of these plant oestrogens is low compared with the natural sex hormones, excessive intakes may affect reproduction adversely, or in limited amounts may have a beneficial effect on fattening animals similar to that of giving synthetic hormones such as stilboestrol and hexoestrol.

Plants containing oestrogenic substances include subterranean clover, Ladino clover, red clover, sweet clover, birdsfoot trefoil and lucerne. The activity of different crops varies with variety, stage of growth and locality.

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SILAGE

Silage is the material produced by the controlled fermentation of a crop of high moisture content. Ensilage is the name given to the process, and the container, if used, is called the silo. The fermentation is controlled either by encouraging lactic acid formation by bacteria present on the fresh herbage, or by direct addition of a weak acid solution or of preservatives such as sodium metabisulphite.

The first method, sometimes referred to as the 'ordinary' process, is the commonest in use, and is dependent upon the fermentation to lactic acid of soluble carbohydrates present in the plant material, resulting in a lowering of pH to within the region of 3.8–4.2. Material of this type is described as 'well preserved silage' and normally has a lactic acid content within the range of 8–12 per cent of the dry matter (Table 17.1). Success in achieving a lactic acid concentration of this level depends upon many factors but basically upon having an adequate supply of soluble carbohydrates.

Silage of pH about 4 will normally remain stable as long as the mass is kept under anaerobic conditions. If however, rain is allowed to enter the silage or if lactic acid concentration is inadequate, then a secondary clostridial fermentation is likely to occur and cause a breakdown of the lactic acid, with the production of butyric acid. Silage of this type has a relatively high pH value, generally above 5, and is described as 'badly preserved' (Table 17.1).

Clostridia require very wet conditions for active development, and it has been found beneficial to wilt crops to a dry matter of 30–50 per cent in the field before ensiling. Wilted crops preserve at higher pH values than wet crops, and consequently a high concentration of lactic acid is of less importance than when wet crops are ensiled.

Another type of material, frequently classed as 'mouldy silage' but more accurately described as putrid or waste material, is produced from herbage in immediate contact with the air. Material of this type is formed on the surface and sides of silos, and its production can be reduced to a minimum by carefully sealing the sides and top of the silo. Waste material should not be given to animals, as it may contain nitrogenous decomposition products which are toxic.

An entirely different process of silage making involves the sterilisation of the mass in the silo by adding chemical sterilisation agents such as formaldehyde, sulphur dioxide or sodium metabisulphite. The success of this method depends largely upon ensuring adequate mixing with the crop, which may often be difficult in practice. If satisfactory sterilisation is achieved, and provided effluent production is not great, the nutritive value of the preserved material should be very similar to that of the original herbage.

Another method of preserving herbage is by the direct acidification of the crop, and the commonest method is the Finnish or A.I.V.

TABLE 17.1. Some Organic Acids of Grass Silages of varying pH Value

pH	(Percentage of dry matter)		
	<i>Acetic acid</i>	<i>Butyric acid</i>	<i>Lactic acid</i>
3.8	1.75	0	8.41
4.0	1.52	0.17	9.29
4.3	0.78	0.19	5.95
4.5	4.70	0.50	5.80
4.7	1.88	1.84	1.08
4.9	4.02	2.25	0.12
5.1	1.92	3.69	1.48
5.2	3.67	4.61	0.69

process, named after the originator A. J. Virtanen. The mixture of acids used in this process varies, but generally consists of hydrochloric and sulphuric acids. These acids are added to material during ensiling in sufficient quantity to lower the pH value below pH 4.0. The resultant product may appear to be a very unnatural food for farm animals, but provided the correct amount of acid is properly distributed throughout the ensiled material no free mineral acids occur. Instead potassium, calcium and magnesium salts are formed by reaction with salts of organic acids present in the original material, and as a result malic, fumaric, citric and other plant acids are liberated. A.I.V. silage has been shown to be palatable and harmless to ruminants even when given as the sole item of diet. The process is not popular in many countries because of the difficulty in handling the strong acids at the time of ensiling.

A number of organic acids or their salts have been used instead of mineral acids for direct acidification in silage making. The commonest is formic acid, which has been used with some success although it has no specific ensiling effect.

A wide variety of crops may be preserved by ensiling, these include grass, grass clover mixtures, legumes, green cereals, kale, root tops, sugar beet pulp, potatoes and fruit residues. Grass, however, is the commonest crop to be made into silage.

FACTORS AFFECTING THE NUTRITIVE VALUE OF GRASS SILAGE

The nutritive value of silage is governed by three main factors (a) chemical changes occurring within the mass, (b) the nature of the crop ensiled, and (c) the degree of effluent production.

(a) *Chemical Changes*

The chemical changes which occur in the crop may be divided into two categories: firstly those taking place immediately after cutting as a result of plant enzyme activity, and secondly those brought about by the action of micro-organisms present on the original herbage or which gain access by contamination after cutting.

(i) *Plant enzymes* In the first category the main changes are caused by aerobic respiration, which will continue, as long as oxygen is present, until the plant sugars are depleted. Sugars are oxidised to carbon dioxide and water, with the production of heat capable of causing a considerable rise in temperature of the mass. If the herbage is not well consolidated during and after filling, then air may permeate into the mass and the temperature will continue to rise. If the rise in temperature is not checked, then an overbeated product, usually dark brown or black in colour, will result. This will be of low feeding value because of an excessive loss of soluble carbohydrate and a lowering of the protein digestibility. The latter may be affected to a marked extent at temperatures above 55°C.

Apart from carbohydrate breakdown, proteolysis also occurs immediately after the herbage is cut. Protein is rapidly broken down and within 24 hours about 16 per cent is degraded to simpler substances, mainly amino acids.

(ii) *Micro-organisms* After aerobic respiration has ceased, microbial changes continue. Fresh herbage contains bacteria on its surface, and these organisms multiply, using the contents of the cells as a medium. As a result of this activity many chemical components of the grass are broken down. Where conditions are favourable for bacteria which produce lactic acid, the acidity of the mass increases until, at about pH 4.0-4.2, organisms other than the aciduric lactic acid bacteria are inhibited as long as conditions remain anaerobic. These aciduric

organisms continue to form lactic acid if soluble carbohydrates are still available, and the pH value may fall to 3.7. At this pH, bacterial growth ceases and the mass remains stable.

Most of the lactic acid is thought to be produced from soluble carbohydrates (sugars and fructosans), although it is known that hemicelluloses can be broken down during ensilage with the production of pentose sugars. These can be fermented by bacteria, but it is unlikely that pentoses are readily available in the initial stages of the ensilage process.

In addition to the production of lactic acid, volatile acids such as formic, acetic, propionic and butyric acids may be formed. Acetic acid is generally present (0.7-4 per cent. of dry matter) even in well preserved silage, since many bacteria produce this acid. Butyric acid is not produced in any quantity in well preserved silage, but is always present in badly preserved material of high pH value; in silage with a pH value above 5.0 butyric acid will be the dominant acid. A butyric acid (clostridial) type of fermentation is liable to occur if the initial soluble carbohydrate content of the herbage is low or if the ensiled material is too wet.

During ensilage about 60 per cent. of the proteins are broken down, even in well preserved material. Where a rapid lactic acid type of fermentation occurs and a satisfactory degree of acidity is produced, the end-products of protein breakdown are mainly amino acids. This breakdown to amino acids is not a disadvantage as far as nutritive value is concerned, but in badly preserved material the amino acids are broken down further to produce various amines such as tryptamine, phenylethylamine and histamine, which are decarboxylated derivatives of tryptophan, phenylalanine and histidine respectively. Betaine, adenine and pentamethylene diamine are typical products of putrefaction and may be present in badly preserved silage. Many of these nitrogenous compounds may be toxic to animals if absorbed into the blood. The final end-product of protein degradation is ammonia, and since this is volatile it may be lost from the silo in gaseous form.

Apart from changes in carbohydrates and proteins, the mineral compounds present in herbage may be altered and potassium, calcium, sodium and magnesium salts of lactic and volatile acids may be formed. So far as is known, the availability of these minerals is not affected. An obvious change is in the colour of the herbage. The brown colour of silage is due to a pigment, phaeophytin, which is a magnesium-free derivative of chlorophyll.

In well preserved silage, where the temperature has not risen to any

appreciable extent, the carotene content should be similar to that of the original crop. Large amounts of carotene can be lost, however, in overheated silages.

As a result of these chemical changes, gaseous losses (mainly of carbon dioxide) occur. The amount of dry matter lost in gaseous form may vary from 5 to 30 per cent, depending upon plant and bacterial enzyme activity. Since these losses are caused by a breakdown of soluble and highly digestible nutrients, it follows that the higher the gaseous loss, the lower will be the feeding value of the silage.

(b) Nature of Crop

The species, stage of growth, physical state and moisture content of the crop ensiled are important factors affecting the nutritive value of the silage. In order to obtain silage of high nutritive value, the crop should be cut at the ear emergence stage of growth, since the final product cannot be better than the original material.

Since the lactic-acid producing bacteria on the ensiled herbage require a supply of fermentable carbohydrates, the sugars and fructosan contents of the original material are very important. The amount of soluble carbohydrate which must be present to ensure a satisfactory type of lactic fermentation depends upon many factors. If the crop is ensiled in a very wet condition or if the initial numbers of lactic acid bacteria on the herbage are low, or if the temperature is allowed to rise excessively as a result of plant respiration, more soluble carbohydrate will be required. High protein grass crops and legumes are difficult to ensile satisfactorily because of low soluble carbohydrate content and because of their high buffering capacity. If the soluble carbohydrate content of the crop is known to be a limiting factor, then a sugar additive, such as molasses, may be sprayed on to the crop at the time of filling the silo.

The physical nature of the crop at the time of ensiling is an important factor in the fermentation process, and it is known that chopping or bruising tends to produce more favourable conditions for micro-organism activity than leaving the material long.

In practice, the herbage being ensiled may be cut over a period of days and in some cases a period of weeks may elapse between the commencement and end of ensiling. This process of delayed filling is undesirable and leads to large losses of nutrients in gaseous form. If filling is delayed, then the nutritive value of the silage may vary throughout the silo. This variation is generally a vertical one, since the top layer is likely to have been made from herbage more mature

and of lower nutritive value than the material in the bottom layers.

The moisture content of the crop at the time of ensiling also has a marked influence on the type of fermentation which occurs. Wet crops containing more than 80 per cent. moisture are difficult to ensile satisfactorily and frequently produce badly preserved material. There is evidence that dry-matter intake on silage diets is related to the moisture content, in that a higher dry-matter intake can be expected when wilted silage is given *ad lib.* than when silage with a higher moisture content is offered. The water *per se* does not appear to be the cause, and it is possible that some compound is formed in low dry matter silage which may affect the animal's appetite.

(c) Effluent Production

In most silos free drainage occurs, and the liquid or effluent produced carries with it soluble nutrients. The amount of effluent produced depends largely upon the initial moisture content of the crop, but it will obviously be increased if the silo is left uncovered so that rain enters. Effluent contains sugars, soluble nitrogenous compounds, minerals, and organic acids produced during fermentation. These nutrients are all highly digestible and are of high nutritive value to the animal. It is obvious that effluent production should be reduced to a minimum, and one way of doing this is to wilt the crop before ensiling.

VALUE TO THE ANIMAL

In terms of its proximate constituents, silage appears to differ little in composition from the original material. Chemically, however, it is a different product (Table 17.2). The nitrogenous constituents are mainly in the form of non-protein nitrogenous compounds, the soluble carbohydrate content is low, generally less than 2 per cent. of the dry matter, and it contains appreciable amounts of lactic and volatile acids. The presence of these acids is nevertheless not deleterious to ruminant animals—many of the components of herbage are fermented in the rumen to volatile fatty acids similar to those present in silage. Lactic acid also may be produced in the rumen, particularly on high sugar or starch diets, although this acid is normally fermented to volatile acids before its absorption. Lactic acid itself is a compound produced in the body during metabolism and can be converted to glucose by the animal. In spite of the chemical changes undergone in well preserved silage, the nutritive value of the final product should be

almost equal to that of the original material (Table 17.2). Badly preserved silage on the other hand is likely to have a lower nutritive value than well preserved silage made from similar material, because of high gaseous production from the breakdown of soluble digestible nutrients and from the deamination of amino acids

TABLE 17.2. Composition and Digestibility of S22 Ryegrass and Silage

(a) Chemical constituents	Composition (percentage of dry matter)	
	Ryegrass	Silage
Protein N	2.66	0.91
Non protein N	0.34	2.08
Volatile N	nil	0.21
Sugars	9.5	2.0
Fructosans	5.6	0.1
Hemicelluloses	15.9	13.7
Cellulose	24.9	26.8
Lignin	8.3	6.2
Lactic acid	nil	8.7
Acetic acid	nil	1.8
(pH)	(6.3)	(3.9)

(b) Proximate constituents and their digestibility	Ryegrass		Silage	
	Composition (per cent of dry matter)	Digestibility coefficient	Composition (per cent of dry matter)	Digestibility coefficient
Organic matter	89.8	77	88.3	75
Crude protein	18.7	78	18.7	76
Ether extract	3.5	64	4.8	72
Crude fibre	23.6	78	25.7	78
Nitrogen free extractives	44.1	78	39.1	72

Although grass silage is regarded primarily as a food for ruminants, when made from young material of low fibre content it may be given to poultry and breeding pigs. It is doubtful, however, if grass silage has any place in the feeding of fattening pigs, because of its relatively low energy value compared with cereal grains. Potato silage is in a different category and can be given satisfactorily to fattening pigs. Results of feeding trials indicate that better growth rates are obtained when the potatoes are steamed before ensiling.

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Chapter 18

HAY, ARTIFICIALLY DRIED GRASS, STRAWS AND CHAFF

HAY

The commonest method of conserving green crops is that of hay-making, the success of which until fairly recently was entirely dependent upon the chance selection of a period of fine weather. The introduction of rapid drying techniques using field machinery and barn drying equipment has, however, considerably improved the efficiency of the process.

The aim in haymaking is to reduce the moisture content of the green crop to a level low enough to inhibit the action of plant and microbial enzymes. The moisture content of a green crop depends on many factors, but may range from about 65 to 85 per cent, tending to fall as the plant matures. In order that a green crop may be stored satisfactorily in a stack or bale, the moisture content must be reduced to about 20 per cent. The custom of cutting the crop in a mature state when the moisture content is at its lowest is clearly a sensible procedure for rapid drying and maximum yield, but unfortunately the more mature the herbage, the poorer is the nutritive value (see Chapter 16).

FACTORS INFLUENCING THE NUTRITIVE VALUE OF HAY

Chemical Changes and Losses during Drying

Chemical changes resulting in losses of valuable nutrients inevitably arise during the drying process. The magnitude of these losses depends to a large extent upon the speed of drying. A number of factors contribute towards these changes.

Action of plant enzymes In warm, dry, windy weather the wet grass, if properly handled and mechanically agitated, will dry rapidly and losses arising from plant enzyme activity will be small. The main losses occur in the soluble carbohydrate fraction as a result of aerobic respiration, in which sugars are oxidised to carbon dioxide and water. This loss results in a concentration of cell wall constituents, especially cellulose and lignin, which is reflected in the higher crude fibre content of the dry matter of hay compared with that of the original herbage.

Table 18 1 shows a comparison in composition and nutritive value between two different haymaking methods, the traditional 'field curing' and the 'tripoding' method. Under poor weather conditions tripoding is likely to result in a better-quality hay, since drying is speeded up. The difference between the two treatments is reflected in the crude fibre contents, and in the digestibility coefficients of the nutrients.

TABLE 18 1 Composition and Nutritive Value of Perennial Ryegrass and of Hay made from it by Two Different Methods in S E Scotland

	<i>Composition</i> (percentage of dry matter)			<i>Digestibility</i> coefficients			<i>Digestible nutrients</i> (percentage of dry matter)		
	<i>Fresh grass</i>	<i>Field cured hay</i>	<i>Tripod hay</i>	<i>Fresh grass</i>	<i>Field cured hay</i>	<i>Tripod hay</i>	<i>Fresh grass</i>	<i>Field cured hay</i>	<i>Tripod hay</i>
Organic matter	93.2	92.5	90.8	76.3	59.1	67.6	71.1	54.7	61.4
Crude protein	12.8	9.9	12.1	63.6	47.3	59.3	8.1	4.7	7.2
Ether extract	2.2	1.4	1.6	43.5	10.9	27.9	1.0	0.2	0.4
Crude fibre	26.9	36.2	32.4	76.8	69.4	75.9	20.6	25.1	24.6
Nitrogen-free extractives	51.3	45.0	44.7	79.9	54.9	65.2	41.0	26.6	29.1
Starch equivalent	—	—	—	—	—	—	62.0	35.4	42.5

Although the major changes during haymaking occur in the carbohydrate fraction, proteins are also likely to be altered by the action of plant enzymes. Immediately after cutting proteolysis occurs, resulting in the formation of amino acids. This change will not affect the value of the crude protein unless the soluble nitrogenous compounds are lost through leaching. The actual crude protein content of hay may be by itself a poor guide to the nutritive value, since it may remain the same, or even increase as a result of losses of other nutrients.

Oxidation When herbage is dried in the field, a certain amount of oxidation occurs. The visual effects of this can be seen in the pigments, many of which are destroyed. The provitamin, carotene, is an important compound affected and may be reduced from 150–200 ppm in the dry matter of the fresh herbage to as little as 2–20 ppm in the hay. Rapid drying of the crop by tripoding or barn drying conserves the carotene more efficiently, and losses as low as 18 per cent in barn

dried hay have been reported. On the other hand sunlight has a beneficial effect on the vitamin D content of hay because of irradiation of the ergosterol present in the green plants.

Leaching Losses due to leaching by rain mainly affect the crop after it has been partly dried. Leaching causes a loss of soluble minerals, sugars and nitrogenous constituents, resulting in a concentration of cell wall constituents which is reflected in a higher crude fibre content. Rain may prolong the enzyme action within the cells, thus causing greater losses of soluble nutrients, and may also encourage the growth of moulds.

Mechanical damage During the drying process the leaves lose moisture more rapidly than the stems. The leaves become brittle and shatter very easily when handled. Excessive mechanical handling is liable to cause a loss of this leafy material, and since the leaves at the bay stage are richer in digestible nutrients than the stems, the resultant hay may be of low feeding value. There are a number of modern machines available which reduce the losses caused by leaf shattering. If the herbage is bruised or flattened, the drying rate of stems and leaves is more similar. Baling the crop in the field at a moisture content of about 45 per cent, and subsequent drying by artificial ventilation, will reduce mechanical losses considerably.

Action of micro organisms If drying is prolonged because of bad weather conditions, changes brought about by the activity of bacteria and fungi may occur. Mouldy hay is unpalatable and may contain substances harmful to animals. It is not uncommon to find patches of mouldy hay in a stack that are due to uneven drying conditions.

Plant Species

The differences in chemical composition between species have already been discussed in Chapter 16. Hay made from legumes is generally richer in protein and minerals than grass hay. Pure clover swards are not commonly grown for making into hay in the United Kingdom, although many 'grass' hays contain a certain amount of clover. Lucerne or alfalfa (*Medicago sativa*) is a very important legume which is grown as a hay crop in many countries. The value of lucerne hay lies in its relatively high content of digestible protein which may be as high as 14 per cent if it is made from a crop cut in the early bloom stage.

Cereals are sometimes cut green and made into hay, and this usually takes place when the grain is at the 'milky' stage. The nutritive values of cereal hays cut at this stage of growth are similar to those of hays made from mature grass, although the protein content

is generally lower. Table 18.2 shows the composition of a number of hays made from different species. These values give no indication of the range in nutritive value. If extremes are considered, it is possible to produce hay of excellent quality with a digestible crude protein of 12 per cent. and a starch equivalent value of 50. On the other hand poor-quality hay made from mature herbage harvested under bad

TABLE 18.2. Composition and Nutritive Value of Hays

(From S. J. Watson and M. J. Nash, 1960, *The Conservation of Grass and Forage Crops*. Oliver and Boyd, Edinburgh)

	No. of samples	(Percentage of dry matter)			
		Crude protein	Crude fibre	Starch equivalent	Digestible crude protein
Meadow	686	11.3	29.8	40.2	6.7
Mixed grass	68	11.4	30.1	39.2	6.3
Cocksfoot (orchard grass)	17	8.2	35.6	31.1	4.2
Fescue	22	9.0	31.5	38.5	4.8
Ryegrass	39	9.6	30.5	41.1	4.8
Timothy	218	7.7	34.1	35.1	3.6
Clover	284	14.3	31.9	37.7	8.9
Lucerne	474	16.5	32.2	36.0	11.8
Vetches	28	21.3	27.7	42.6	16.3
Barley	19	9.3	26.5	40.8	5.2
Oat	48	8.0	32.9	35.3	4.1
Wheat	20	8.2	26.8	36.5	4.4

weather conditions may have a negative digestible crude protein content and a starch equivalent as low as 20; material of this type is little better in feeding value than oat straw.

Stage of Growth

The stage of growth of the crop at the time of cutting is a very important factor in determining the nutritive value of the conserved product. The later the date of cutting, the larger will be the yield, the lower the digestibility and net energy value, and the lower the voluntary intake of hay by animals. It follows therefore that, provided the drying processes are similar, then hays made from early-cut crops will be of higher nutritive value than hays made from mature crops. Unfortunately losses may be high in making hay from young herbage because of its relatively high moisture and soluble nutrient content.

The question of when to cut herbage for hay is a complex one, depending upon many factors. The economics of harvesting must be considered, since a greater number of operations may be required if a

crop is cut too early. Furthermore other factors are important, for example whether the hay is to be given as a sole food or with concentrates, and whether the hay is required for maintenance over a winter period or for rapidly growing, fattening, or milk-producing animals.

Changes in the Stack

The chemical changes and losses associated with haymaking do not completely cease when hay is stored in the stack or barn. The stored crop may contain from 10 to 30 per cent. moisture. At the higher moisture levels chemical changes brought about by the action of plant enzymes and micro-organisms are likely to occur. There may be oxidative degradation of sugars, although hexoses may also combine with amino acids or proteins. This chemical combination is probably partly responsible for the dark-brown colour observed in overheated hays. Browning has been observed at temperatures as low as 32° C.

Respiration ceases at about 40° C, but the action of thermophilic bacteria may go on up to about 72° C. Above this temperature chemical oxidation can cause further heating. The heat tends to accumulate in hay stored in bulk, and eventually combustion may occur.

Losses of carotene during storage depend to a large extent on the temperature. Below 5° C little or no loss is likely to occur, whereas in warm weather losses may be considerable.

The changes that take place in the stack are likely to result in a lowering of nutritive value and an increase in the proportion of cell wall constituents. The feeding value of heated hays is relatively low, since high temperatures lower the digestibility of proteins. Digestibility coefficients for protein as low as 2.6 per cent. have been reported for 'black overheated' hay.

The changes which take place in the stack depend to a large extent on the moisture content of the hay at the time of storing. If the moisture in the stored crop is less than 10 per cent., then little or no change will take place during storage.

ARTIFICIALLY DRIED GRASS

Dried grass is defined in the Fertilisers and Feeding Stuffs Regulations 1960 (amended 1964) as follows

'Any product, whether ground or not, which (a) is obtained by artificially drying any of the following—grass, clover, lucerne, sainfoin, green cereals or any mixture consisting of any of them, and (b) is otherwise as grown (that is to say including any growths harvested therewith but with no other substances added thereto), and contains not less than 13 per cent protein calculated on the assumption that it contains 10 per cent moisture'

A poorer quality of dried grass, termed 'dried grass (maintenance quality)', refers to dried herbage which contains less than 13 per cent. but not less than 10 per cent. crude protein, calculated on the assumption that it contains 10 per cent. moisture. Dried herbage containing less than 10 per cent. crude protein is designated 'dried green roughage'.

In the production of dried grass, the drying is brought about by allowing the fresh herbage to meet gases at a high temperature. The temperature of the gases depends upon the type of drier used. In the 'low temperature' type of drying equipment, the hot gases are usually at a temperature of about 150° C and the drying time is about 20–40 minutes. With 'high temperature' driers, the temperature of the gases is initially within the range of 500°–1000° C and drying takes place in a matter of 6–10 seconds.

The temperature and time of drying are very carefully controlled so that the grass is never completely desiccated, and the final product usually contains about 5–10 per cent. moisture. As long as some moisture remains in the material, the temperature of the grass is unlikely to exceed 100° C. It is obvious, however, that if the grass is left in contact with the hot gases too long the material would be charred or even completely incinerated.

Changes in nutritive value. Artificial drying, if carried out properly, has very little effect upon the nutritive value of the crop. This can be seen from the results presented in Table 18.3. The dry matter losses from mechanical handling and drying are together not likely to exceed 10 per cent. It follows that the nutritive value of artificially dried grass depends upon the composition of the original fresh crop, and such factors as stage of growth, species and manurial treatment, already discussed in Chapter 16, will be important.

Very young leafy materials have high digestible crude protein and net energy values, but contain more moisture than mature crops. The initial moisture content of the crop is a very important factor in the economies of grass drying. Dried grass is usually graded and sold on its crude protein content, and the aim is to obtain a product of high protein content. A classification system based on crude protein content has been suggested by the National Agricultural Advisory Service and is given in Table 18.4.

Vitamins in dried grass. The drying process is known to destroy most of the vitamin C in grass, but since farm animals have no need of a dietary source of this vitamin its loss is of no practical importance. The carotene content of dried grass has always been of great importance, and until fairly recently in the United Kingdom the product

was graded and sold on carotene content. The loss of carotene during drying rarely exceeds 10 per cent, but loss of this provitamin is likely to occur during the storage of dried grass, especially if exposed

TABLE 18 3 Composition and Digestibility of Fresh Grass and Artificially Dried Grass
(From S J Watson, 1951, *Grassland and Grassland Products* Arnold, London)

	Fresh grass		Artificially dried grass	
	Composition of dry matter (per cent)	Digestibility (per cent)	Composition of dry matter (per cent)	Digestibility (per cent)
Ether extract	3.08	52.3	3.38	67.8
Crude fibre	27.24	82.2	25.29	83.4
Crude protein	14.79	74.0	15.02	72.8
Ash	9.23	—	10.08	—
Nitrogen free extractives	45.66	78.2	46.23	81.3
Dry matter	100.00	74.4	100.00	77.4

to light and air, dried grass meal can lose as much as half its carotene during 7 months' storage under ordinary commercial conditions. A high quality meal should have a carotene content of about 250 ppm, although under exceptional conditions carotene contents as high as

TABLE 18 4 Classification of Dried Grass
(From *Rations for Livestock* Bulletin of the Ministry of Agriculture, Fisheries and Food No 48, H M S O 1960)

Category	Crude protein (90 per cent dry matter basis)
A	17 or over
B	15-16.9
C	13-14.9
D	11-12.9
Super hay	Under 11.0 (maintenance food)

450 ppm have been obtained. The vitamin D content of dried grass is very low, since the drying process does not allow irradiation of sterols to take place.

Feeding value Dried grass made from young herbage is a valuable product in the diet of farm animals, especially of those on winter rations, since it provides a green food rich in carotene, protein and digestible energy. Because of the relatively high costs of production dried grass is generally given in limited quantity as a concentrate to

ruminant animals. Small quantities (3-5 per cent.) of high-quality dried grass are frequently included in the diets of pigs and poultry, primarily as a source of vitamins. The product is also valuable for laying hens as a source of pigments which produce a satisfactory colour of egg yolk.

Dried grass meal by itself is not very acceptable owing to its dusty nature, and it is customary either to moisten it before feeding or preferably to mix it with other foods. Frequently dried grass is made into cubes or pellets, which are easier to handle and are more palatable to stock.

Dried Lucerne

In the U.S.A. considerable amounts of lucerne (alfalfa) are artificially dried and sold as a high-vitamin feed-supplement for broilers. As the production of this is seasonal large volumes of dried meal must be stored for periods of six months or more, and unless precautions are taken losses of carotene, xanthophyll and vitamin E are liable to occur as a result of oxidation. Since the rate of loss is a function of temperature, large volumes were stored under refrigeration in the past. More recently the dried product has been stored satisfactorily under inert gas, which virtually eliminates oxidative losses up to the time of removal from storage. Many manufacturers also add anti-oxidants which protect the product from the time it is removed from the inert gas until it is used.

STRAWS AND CHAFF

Straws consist of the stems and leaves of plants after the removal of the ripe seeds by threshing, and are produced from most cereal crops and from some legumes. Chaff consists of the husk or glumes of the seed which are separated from the grain during threshing.

These products are extremely fibrous, rich in lignin and of extremely low nutritive value. They should not be used as pig or poultry foods.

Cereal Straws

During the ripening process nutrients are transferred from the stems and leaves to the grain, so that the composition of the straws is to a large extent dependent upon the degree of ripeness at the time of cutting. The stem is very variable in composition, the lower parts being more fibrous and poorer in feeding value than the heads.

Oat straw. Of the cereal straws, oat straw is generally regarded as having the highest feeding value, and it is popular in certain areas as a

bulky food for store cattle along with roots and concentrates. It is also used in limited quantities as a source of fibre for dairy cows. Oat straw is superior to other cereal straws largely because the crop is usually cut before the grain is fully ripe. Varietal differences in composition between samples of oat straw grown under similar conditions and harvested at comparable stages of ripeness are negligible, any variations in composition being mainly caused by environmental factors. The protein content of oat straws is generally very low, usually about 3-5 per cent. As a general rule in the United Kingdom the actual content increases with latitude towards the north, being highest in Scotland and lowest in southern England, this is because oats grown under cold and wet conditions do not mature completely. The apparent digestibility of the protein is also very low, and will be negative if the metabolic nitrogen excreted is greater than the nitrogen absorbed from the gut. This is usually the case with roughages at about the 3-4 per cent crude protein level. Pepsin digestion determinations made in the laboratory, however, indicate that a large part of the straw protein (53-76 per cent) may be digested by ruminant animals. As might be expected, the crude protein content can be increased by the application of nitrogenous fertilisers. The protein content is not affected greatly by the method of harvesting and there is little difference in content between 'binder-cut' straw and 'combine cut' straw.

Crude fibre constitutes as much as 35-45 per cent of straws, and this has a digestibility coefficient of about 55-60 for ruminants. The fibre content of combine cut ripe straw is frequently higher than that of straw cut with the binder, a reflection of the later harvesting of the combine cut crop.

Oat straw contains some sugars, generally 2-4 per cent, although some samples grown in northern Scotland have contained as much as 9 per cent. The main sugar present is fructose.

The ash content is variable (3.9 per cent), and there is evidence that soluble minerals may be leached out of the straw under very wet conditions of harvesting. The ash contains about 30 per cent of silica, which has no nutritional value, and about 20 per cent of potassium, the main essential element present. Both calcium and phosphorus contents are low, although the straw contains more calcium than the grain.

The digestibility of the organic matter by ruminants rarely exceeds 50 per cent, and because of this and its fibrous nature the net energy value of oat straw is very low. The Starch Equivalent value attributed to this roughage is usually 10-20.

Barley straw If the crop is cut when the grain is ripe, then the straw is of poor feeding value, if however the cereal is harvested early, then the straw is similar to oat straw in nutritive value

A disadvantage in the feeding of both barley and oat straw to ruminant animals is the low voluntary intake of these materials. Whereas a cow will consume up to 22 lb of medium-quality hay, it will only eat about 10 lb of straw. These low intakes of straws are associated with their low levels of digestibility, especially of the cellulose. A limiting factor in the bacterial degradation of cellulose is the low nitrogen content of the straw. Organic matter digestibility can be increased considerably by the addition of nitrogen in the form of either protein or urea. Studies in which 150 g/day of urea were infused into the rumen of cows showed that the digestibility of the organic matter increased from 41 to 50 per cent while the voluntary intake increased by about 40 per cent.

Other cereal straws Wheat and rye straws are not usually given to animals because of their very low feeding value, and are more useful on the farm as bedding materials.

Legume Straws

The straws of beans and peas are richer in protein, calcium and magnesium than the cereal straws, and if properly harvested are useful roughage foods for ruminant animals. Because of their thick fibrous stems they are more difficult to dry than cereal straws and frequently become mouldy on storage.

Chaff

Cereal chaff is similar to straw in being a fibrous food, but is generally more digestible and richer in protein content. The most valuable is oat chaff. Care is required in feeding animals on barley chaff because of the presence of the awns, whose serrated edges may cause irritation to the animal.

FURTHER READING

- S J WATSON AND M J NASH 1960 *The Conservation of Grass and Forage Crops*
Oliver and Boyd Edinburgh
F B MORRISON, 1959 *Feeds and Feeding* Morrison Publishing Co, Iowa

ROOTS AND TUBERS

The root crops include turnips, swedes, mangolds, fodder beet, carrots and parsnips. Potatoes and Jerusalem artichokes are frequently classified as root crops, although they are in fact tubers and are chemically different from the roots. Whereas the main component of the dry matter of root crops is sugar, tubers contain either starch or fructosans as the main component.

Roots

The main characteristics of root crops are their high moisture content (75–92 per cent) and relatively low crude fibre content (5–11 per cent of the dry matter). The nitrogen-free extractives content of the dry matter is high, is rich in sugars, mainly sucrose, and is highly digestible by ruminants. Roots are not a popular food for pigs and poultry because of their bulky nature, although some which have higher dry matter contents such as fodder beet are given to pigs. The crude protein content of roots is within the range of 4–12 per cent of the dry matter, and a fairly high proportion of this fraction is in the form of non protein nitrogenous compounds. Roots are not good sources of calcium and phosphorus, but are particularly rich in potassium.

The most variable constituent of the root crops is the dry matter content, and this is the main factor influencing their nutritive value. With foods containing about 10 per cent of dry matter a difference of only 2 units will alter the feeding value by 20 per cent.

Factors Affecting the Composition and Nutritive Value of Roots

Species Turnips, on average, have the lowest dry matter content, and sugar beet the highest. Table 19.1 shows the variation in composition of the main root crops.

Variety Varietal differences occur. This is particularly true of the species *Beta vulgaris*, which includes mangolds, fodder beet and sugar beet. The varieties form a continuous series from mangolds to sugar beet with dry matter contents ranging from 9 to 25 per cent. Varietal

differences in other species are not so great and generally do not exceed 2 units of dry matter

Size of root Experiments in which small roots have been compared with large ones taken from the same field indicate that the small

TABLE 19 1 Ranges of Major Constituents of Roots

	Dry matter (per cent)	Percentage of dry matter		
		Crude protein	Crude fibre	Sugars
Turnips	6-10	7-13	5-13	50-61
Swedes	8-12	7-12	5-13	50-63
Mangolds	9-14	8-10	4-6	55-65
Fodder beet	14-22	6-8	4-6	60-70
Sugar beet	22-25	4-6	4-6	65-75

root has a higher dry matter and higher crude fibre content than the large root. Differences also occur in digestibility (Table 19 2), the more fibrous smaller root being of lower digestibility.

The variations in dry matter content due to size may be quite appreciable. For example mangolds can vary in weight from about 1 to 7 lb,

TABLE 19 2 Composition and Digestibility of Large (Mean Fresh Weight 3 lb) and Small (Mean Fresh Weight 1 lb) Swedes, Harvested from the Same Plot

		Percentage of dry matter					
	Dry matter	Organic matter	Crude protein	Ether extract	Crude fibre	Nitrogen free extractives	Starch equivalent
<i>Composition</i>							
Large	10.3	93.9	8.5	0.7	11.2	73.5	—
Small	11.4	94.6	7.1	0.6	12.7	74.2	—
<i>Digestibility coefficients *</i>							
Large	—	90.5	64.5	47.0	80.5	95.4	—
Small	—	84.7	41.6	37.7	61.4	92.9	—
<i>Digestible nutrients</i>							
Large	—	85.0	5.5	0.3	9.0	70.1	72.0
Small	—	80.1	3.0	0.2	7.8	68.9	68.0

* For sheep

and it has been shown that over this range the dry matter may vary from 11 to 14 per cent within the same variety.

Season The variations in composition due to season may be quite large. Generally, low dry matter roots are produced in a wet season and relatively high dry matter roots in a hot dry season.

Storage Changes in composition occur in roots during storage. These changes are influenced by the condition of storage, but generally the dry matter content decreases. Dry matter losses of up to 10 per cent over the winter are not uncommon.

Turnips and Swedes

Turnips (*Brassica rapa*) and swedes (*Brassica napobrassica*) are chemically very similar, although turnips contain less dry matter than swedes (Table 19.1). The starch equivalent value of turnips on a dry matter basis is between 52 and 55, whereas that for swedes is 62 to 70. The latter is higher than the value given for turnips partly because of the slightly higher digestibility of swedes and partly because of the different 'V' or conversion numbers that Kellner gave to these two species. The respective values for swedes and turnips are 85 and 77. It is impossible to say whether these relatively large differences apply generally, and there may be some doubt, since American workers have assessed the net energy values of turnip and swede dry matter as 839 kcal and 856 kcal per lb respectively, i.e. with a difference of only 2 per cent.

Both turnips and swedes are liable to taint milk if given to dairy cows at or just before milking time. The volatile organic compound responsible for the taint is absorbed from the air by the milk and is not passed through the cow.

Swedes and turnips may be given to all classes of farm animals, but are mainly used for cattle and sheep.

Mangolds, Fodder Beet and Sugar Beet

Mangolds, fodder beet and sugar beet are all members of the same species, *Beta vulgaris*, and for convenience they are generally classified according to their dry matter content. Mangolds are the lowest in dry matter content, richest in crude protein and lowest in sugar content of the three types. Fodder beet can be regarded as lying in between mangolds and sugar beet in terms of dry matter and sugar content, while sugar beet is richest in dry matter and sugar content, though poorest in crude protein. On a dry matter basis the starch equivalent value of mangolds is similar to that of turnips, and the starch equivalent of sugar beet about the same as that of swedes.

Mangolds 'Low dry matter' mangolds have a dry matter content between 9 and 12 per cent and are similar to turnips in composition and nutritive value. 'Medium dry matter' mangolds have a dry matter content of 12 to 14 per cent. This group are usually smaller in size than the low dry matter group, but usually develop fairly large tops.

It is customary to store mangolds for a few weeks after lifting, since freshly lifted mangolds may have a slightly purgative effect. The toxic effect is associated with the nitrate present, which on storage is converted into asparagine. Unlike turnips and swedes, mangolds do not cause milk taints when given to dairy cows.

Fodder beet. 'Medium dry matter' fodder beet contains from 14 to 18 per cent. of dry matter, whereas the 'high dry matter' varieties may contain up to 22 per cent.

Fodder beet is a popular food in Denmark and the Netherlands for dairy cattle and young ruminants. Care is required in the feeding of high dry matter fodder beet to cattle, since excessive intakes may cause digestive upsets, hypocalcaemia and even death. The digestive disturbances are probably associated with the high sugar content of the root.

The use of fodder beet as the bulk ration for feeding pigs has given satisfactory results, but experiments have shown that the fattening period is slightly longer than when sugar beet is used. The digestibility of the organic matter of fodder beet is very high (about 90 per cent.).

Sugar beet. Most sugar beet is grown for commercial sugar production, though it is sometimes given to animals, especially cows and pigs. Because of its hardness the beet should be pulped or chopped before feeding.

After extraction of the sugar at the sugar beet factory, two valuable by-products are obtained which are given to farm animals. These are sugar beet pulp and molasses.

Sugar beet pulp. The sugar beet on arrival at the factory is washed, sliced and soaked in water, which removes most of the sugars. After extraction the residue is called sugar beet pulp. This product contains 80-85 per cent. of water and it may be sold in the fresh state for feeding farm animals, but because of transport difficulties it is frequently dried to 10 per cent. moisture content. Since the extraction process removes the water-soluble nutrients, the dried residue consists mainly of cell wall polysaccharides, and consequently the crude fibre content is relatively high (about 18 per cent.); the crude protein and phosphorus contents are low, the former being about 9 per cent. Beet pulp is extensively used as a food for dairy cows and is also given to fattening cattle and sheep. It is not a popular food for pigs, especially fattening pigs, because of its fibrous nature, and is not suitable for poultry.

Beet molasses. After crystallisation and separation of the sugar from the water extract, a thick black liquid termed molasses remains.

This product contains 70–75 per cent of dry matter, of which about 65 per cent consists of sugars. The molasses dry matter contains only 2–4 per cent of crude protein, most of this being in the form of non-protein nitrogenous compounds, including the amine, betaine, which is responsible for the 'fishy' aroma associated with the extraction process.

Molasses is a very laxative food and is given to animals in small quantities. Frequently the molasses is added to the beet pulp, which is then marketed as 'dried molassed beet pulp'. A variety of products containing molasses are available. Absorbents used with molasses include bran, brewers' grains, malt culms, spent hops and sphagnum moss. The nutritive value of these molassed products will depend upon the absorbent used.

Molasses is used, generally at levels of 5–10 per cent, in the manufacture of compound cubes and pellets. The molasses not only improves the palatability of the product but also acts as a biogenic agent. Since molasses is a rich and relatively cheap source of soluble sugars it is often used as an additive in silage making.

Carrots and Parsnips

Carrots (*Daucus carota*) are not grown on a large scale for feeding to farm animals, largely for economic reasons, but they are a valuable food for all classes of farm animals, being particularly favoured as a food for horses. Carrots contain 11–13 per cent dry matter, which has a starch equivalent value of about 70.

Parsnips (*Pastinaca sativa*) are slightly richer in dry matter than carrots but the dry matter has a similar starch equivalent value. The carrot is rich in carotene, and this provitamin is also present in parsnips.

TUBERS

Potatoes

Potatoes (*Solanum tuberosum*) differ from the root crops in that the main component is starch and not sucrose. The starch content of the dry matter is about 70 per cent (see Table 19.3), this carbohydrate is present in the form of granules which vary in size depending upon the variety.

The crude protein content of the dry matter is approximately 10 per cent., about half of this being in the form of non-protein nitrogenous compounds. One of these compounds is a toxic substance, solanine, which may cause gastroenteritis in animals. Solanine levels may be high in potato tubers exposed to light. Associated with light

exposure is greening due to the production of chlorophyll. Green potatoes should be regarded as suspect, although removal of the eye and peel, in which the solanine is concentrated, will reduce the toxicity. Young shoots are also likely to be rich in solanine and these should be removed and discarded before feeding. Immature potatoes have been found to contain more solanine than mature tubers. The toxic risk is reduced considerably if potatoes are steamed or otherwise cooked, the water in which the tubers have been boiled being discarded.

TABLE 19.3. Percentage Composition of the Potato Tuber
(From W. G. Burto, 1948, *The Potato*. Chapman and Hall, London)

	Range	Mean
Dry matter	19.0-24.6	22.0
<i>Percentage of dry matter</i>		
Starch	67.9-81.0	71.6
Reducing sugars	0.25-0.44	0.33
Sucrose	0.76-1.05	0.91
Total N	1.15-1.99	1.60
Protein N	0.59-0.87	0.74
Fat	0.29-0.47	0.38
Fibre	1.3-7.4	4.04
Ash	4.1-6.1	5.07

The fibre content of potatoes is very low, which makes them particularly suitable for pigs and poultry. The best results are obtained if the tubers are cooked or steamed, since raw potatoes have laxative properties when given to pigs and poultry. It is unnecessary, however, to cook potatoes for ruminants.

The dry matter of potatoes has a higher energy value than that of the root crops. The starch equivalent value of the dry matter is within the range 77-84, while the digestible energy value of the dry matter of cooked potatoes for pigs is about 1750 kcal/lb.

Potatoes are a poor source of minerals, except of the abundant element potassium, the calcium content being particularly low. The phosphorus content is rather higher since this element is an integral part of the potato starch molecule, but some 20 per cent. of it is in the form of phytates (see p. 79).

During the storage of potatoes considerable changes in composition may occur. The main change is a conversion of some of the starch to sugar and the oxidation of this sugar, with the production of carbon dioxide during respiration. The respiration rate increases with an increase in temperature. There may also be a loss of water from the tubers during storage.

Dried potatoes. The difficulty of storing potatoes satisfactorily for any prolonged period of time has led to a number of processing methods. Several methods of drying are used. In one method the cooked potatoes are passed through heated rollers to produce dried potato flakes. In another method sliced tubers are dried direct in flue gases; the resultant potato slices are frequently ground to a meal before marketing. The products are valuable concentrate foods for all classes of animals.

Other Tubers

The only other tuber of some importance in the feeding of farm animals is the Jerusalem artichoke. This, like potatoes, is very low in fibre. The main carbohydrate is the fructosan, inulin, instead of starch as in the potato. The tubers do not store well and have never been a popular food for farm animals.

FURTHER READING

- F. B. MORRISON, 1959. *Feeds and Feeding* Morrison Publishing Co., Iowa.
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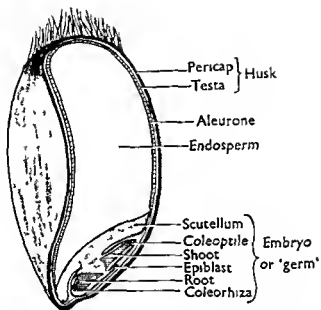


FIG 20 1. Longitudinal section of caryopsis (grain) of wheat

CEREAL GRAINS AND CEREAL BY-PRODUCTS

The name 'cereal' is given to those members of the Gramineae which are cultivated for their seeds. Cereal grains are essentially carbohydrate concentrates, the main component of the dry matter being starch. The dry matter content of the grain depends on the harvesting method and storage conditions but is generally within the range of 82-90 per cent.

The crude protein is the most variable component, usually ranging from 8 to 12 per cent., although some varieties of wheat contain as much as 22 per cent. Of the nitrogenous components 85-90 per cent. are in the form of proteins, but these are deficient in certain essential amino acids, particularly lysine and methionine. Recently it has been shown that the value of cereal proteins for promoting growth in young chicks is in the order: oats>barley>maize or wheat. The high relative value of oat protein for growth is probably due to its slightly higher lysine content.

The oil content of cereal grains varies with species, oats being the richest (5 per cent.) and wheat the poorest (2 per cent.). The embryo or 'germ' contains more oil than the endosperm (see Fig. 20.1); in wheat, for example, the embryo has 10-17 per cent. oil while the endosperm contains only 1-2 per cent. The embryo of rice is exceptionally rich in oil, containing as much as 35 per cent. Cereal oils are unsaturated, the main acids being linoleic and oleic, and because of this they tend to become rancid quickly, and also produce a soft body fat. This is particularly true of oats and maize, which contain more than twice as much oil as barley and wheat.

The crude fibre content of the harvested grain is highest in those such as oats or rice which contain a husk or hull formed from the inner and outer paleae, and is lowest in the 'naked' grains, wheat and maize. The husk has a diluent effect on the grain as a whole and reduces the energy value proportionally. Of the grains as harvested, oats have the lowest metabolisable energy value and maize the highest, the respective values (kcal/lb) for poultry being 1080 and 1510. These differences are also reflected in the starch equivalent values for ruminants, which are about 60 and 78 respectively.

Starch occurs in the endosperm of the grain in the form of granules, whose size and shape vary with different species. Cereal starches consist of about 25 per cent amylose and 75 per cent amylopectin, although 'waxy' starches contain greater amounts of amylopectin.

The cereals are all deficient in calcium, containing less than 0.1 per cent. The phosphorus content is higher, being 0.3-0.4 per cent, but part of this is present as phytates (see Chapter 79). Cereal phytates have the property of being able to immobilise dietary calcium and probably magnesium, oat phytates are more effective in this respect than barley, rye or wheat phytates. The cereal grains are deficient in vitamin D and, with the exception of yellow maize, in provitamins A. They are good sources of vitamin E and thiamine, but have a low content of riboflavin. Most of the vitamins are concentrated in the aleurone layer and the germ of the grain.

Calves, pigs and poultry depend upon cereal grains for their main source of energy, and at certain stages of growth as much as 90 per cent of their diet may consist of cereals and cereal by products. Cereals generally form a lower proportion of the total diet of ruminants, although they are the major component of the concentrate ration.

OATS (*Avena sativa*)

The oat has always been a favourite cereal for ruminant animals and horses, but has been less popular in pig and poultry feeding because of its comparatively high fibre content and low energy value.

The nutritive value of oats depends to a large extent on the proportion of kernel (groat) to hull. The percentage of hull in the whole grain depends upon the variety, environment, and season, and can vary from 23 to 35 per cent (average 27 per cent). Oats of high hull content are richer in crude fibre and have a lower metabolisable energy value than low hulled oats.

The crude protein content which ranges from 8 to 15 per cent, is increased by the application of nitrogenous fertilisers. Oat proteins are of poor quality and are deficient in the essential amino acids methionine, histidine and tryptophan, the amount of each of these acids in oat protein being generally below 2 per cent. The lysine content is also low but is slightly higher than that of the other cereal proteins. Glutamic acid is the most abundant amino acid of oat protein, which may contain up to 20 per cent.

The oil content of oats is high compared with that of the other cereal grains, and about 60 per cent of it is present in the endosperm.

As mentioned earlier, the oil is rich in unsaturated fatty acids and has a softening effect on the body fat.

Oats are usually given 'crushed' or 'bruised' to cattle and sheep but ground to pigs and poultry. It is frequently stated that oats should be very finely ground for pigs since fine grinding increases the digestibility. Recent experiments do not support this view, however, and grinding need only be sufficient to prevent the husk forming a physical barrier to the action of the digestive juices. Growth and digestibility trials with pigs of between 70 lb and half grown weight have shown that there is no advantage in finer grinding than is attainable by ordinary farm grinding equipment.

Oat By-products

During the commercial preparation of oatmeal for human consumption, a number of by-products are obtained which are available for animal feeding. When the oats are received at the mill they contain a number of foreign grains, mainly other cereals and weed seeds, which are removed as cockle before processing. The cleaned oats are then generally dried before passing on to the huller, which removes the husks. During the hulling process three by-products are obtained: the husks or hulls, oat dust and meal seeds. Oat dust consists of the hairs that lie between the oat and the hull. Meal seeds are the husks and part of the endosperm of the small grains. With good milling the amount of meal seeds produced is very low. They are very variable in composition and may be designated 'coarse', with a crude fibre content of about 28 per cent., to 'fine', with a crude fibre content of about half this value; the crude protein may also vary from about 3 to 9 per cent. The hulls form the main by-product in terms of quantity, but these are of very low feeding value, being little better than oat straw. Their crude protein content is so low (about 2 per cent.) that in digestibility studies negative digestibility coefficients for nitrogen are likely to be obtained, owing to the relatively high amount of metabolic nitrogen excreted compared with that digested from them. The crude fibre content is usually between 33 and 36 per cent., which makes the by-product valueless as food for animals other than ruminants.

Oat hulls may be combined with oat dust in the proportion in which they come from the mill (4 to 1) to produce a product sold as 'oat feed'. This material is rather better in feeding value than the hulls alone. In the United Kingdom oat feed should not, by legal definition, contain more than 27 per cent. crude fibre. An alternative use for the hulls is in the brewing industry, where they are often added to the malt to assist in the drainage of wort from the mash tun.

The dehusked oats themselves (kernels or groats) are of high nutritive value, containing about 16 per cent crude protein and less than 2 per cent crude fibre. The groats are generally too expensive to give to farm animals, and are ground into oatmeal after removal of the tips. The tips are mixed with any residues which accumulate during the flow of the oats during milling and the product is designated 'flowmeal'. Flowmeal can be a very valuable food since it may contain the germ, most of this by product, however, is absorbed by the compound trade

BARLEY (*Hordeum sativum*)

Barley has always been a popular grain in the feeding of farm animals, especially pigs. In most varieties of barley the kernel is surrounded by a hull, but the hull forms a much lower percentage of the grain (10-14 per cent) than in oats, so that barley has consequently a lower crude fibre content.

The crude protein of barley grain ranges from about 6 to 13 per cent, with average values of 9 to 10 per cent. As with oats, the protein is of low quality. The oil content is relatively low, generally less than 2 per cent. Barley forms the main concentrate food for fattening pigs in the United Kingdom, producing a good carcass with a hard fat of high quality.

Because of the lower proportion of hull to kernel, barley has a higher net energy value than oats. In recent years experiments have shown that beef cattle can be fattened on concentrate diets consisting of about 85 per cent bruised barley without the use of roughages. In this process the barley is usually treated so that the husk is kept intact and at the same time the endosperm is exposed, the best results are obtained by rolling grain of a moisture content of 16-18 per cent. Certain hazards, such as bloat, can be encountered with this type of feeding, and care is required. It is important that a protein concentrate with added vitamins A and D and minerals be used to supplement high cereal diets of this type.

Barley By products

By products of the brewing industry In brewing, barley is first soaked and allowed to germinate. During this process, which is allowed to continue for about 6 days, there is development of a complete enzyme system for hydrolysing starch to dextrins and maltose. Although the enzymatic reactions have been initiated in this germination or 'malting' process, the main conversion of the starch in the grain to maltose and

other sugars takes place during the next process, described as 'mashing'. After germination but before mashing, the grain or malt is dried, care being taken not to inactivate the enzymes. The sprouts are removed and are sold as malt culms or coombs. The dried malt is crushed, and small amounts of other cereals such as maize or rice may be added. Some fibrous material, such as oat hulls, is commonly added to facilitate drainage. Water is sprayed on to the mixture and the temperature of the mash increased to about 65° C.

The object of mashing is to provide suitable conditions for the action of enzymes on the proteins and starch, the latter being converted to dextrins, maltose and small amounts of other sugars. After the mashing process is completed the sugary liquid or 'wort' is drained off, leaving 'brewers' grains' as a residue. Brewers' grains may be sold for feeding farm animals either in the wet state or they may be dried.

The wort is next boiled with hops, which give it a characteristic flavour and aroma; the hops are then filtered off and after drying are sold as spent hops. The wort is then fermented in an open vessel with yeast for a number of days, during which time most of the sugars are converted to alcohol and carbon dioxide. The yeast is filtered off, dried, and sold as brewers' yeast.

The by-products obtained from the brewing process are therefore: malt culms, brewers' grains, spent hops and brewers' yeast.

Malt culms. Malt culms consist of the plumule and radicle of barley, and are relatively rich in protein (about 24 per cent. crude protein). They are not a high-energy food, however, and because of their fibrous nature their use is generally restricted to the feeding of ruminants and horses. Malt culms absorb water readily, and since they tend to swell in the stomach are usually moistened before they are given to animals.

Brewers' grains. Brewers' grains or 'draff' consist of the insoluble residue left after removal of the wort. In addition to the insoluble barley residue this product may contain oat hulls, maize and rice residues. The fresh brewers' grains contain about 70-75 per cent. water, and are sometimes given to cattle, sheep and horses in this form; frequently the wet product is dried to about 10 per cent. moisture, since in the fresh state it does not store well. Dried brewers' grains contain about 18 per cent. crude protein and 15 per cent. crude fibre, although the composition will vary according to the nature and amount of additives used. Brewers' grains have always been a popular food for dairy cows, but they are of little value to poultry and are not very suitable for pigs except in small amounts.

Spent hops. Dried spent hops are a fibrous product and can be compared to poor hay in nutritive value, but are less palatable, probably because of their bitter flavour. This product is rarely used as a food for animals today, most of it being sold for use as fertiliser.

Dried brewers' yeast. Dried yeast is a rich protein concentrate containing about 42 per cent of crude protein. It is highly digestible and may be used for all classes of farm animals. The protein is of fairly high nutritive value and is specially favoured for feeding pigs and poultry. It is a valuable source of many of the B group of vitamins, is relatively rich in phosphorus but has a low calcium content. Unfortunately this product is not relished in large quantities by animals, probably because of its bitter flavour, and is usually given in restricted amounts at levels not exceeding 10 per cent of the diet. It is difficult to persuade cows to eat yeast, but sheep, pigs and poultry consume it more readily. The vitamin D content is sometimes increased by irradiation.

Distillers' grains. In distilling, the soluble materials may be extracted, as in brewing, or the whole mass fermented, the alcohol then being distilled off. The residue after filtration is sold as wet or dried distillers' grains. In addition to barley other grains may be used in this process, and the composition of the residue after fermentation and distillation will obviously vary depending on the original mixture. Dried distillers' grains are often richer in protein than dried brewers' grains. Distillers' grains may be given to cattle and sheep, but they are not popular foods for pigs and poultry because of their fibrous nature.

By products of the pearl barley industry. In the preparation of pearl barley for human consumption, the bran coat is removed and the kernel is polished to produce a white shiny grain. During this process three by products described as coarse, medium and fine dust, are produced and these are frequently mixed and sold as barley feed. Barley feed contains about 13 per cent crude protein and about 9 per cent crude fibre. The amount of this product available in this country is very small.

WHEAT (*Triticum aestivum*)

Wheat grain is very variable in composition. The crude protein content, for example, may range from 6 to 22 per cent, though it is normally between 8 and 14 per cent. Climate and soil fertility as well as variety influence the protein content. The amount and properties of the proteins present in wheat are very important in deciding the

quality of the grain for flour production. The most important proteins present in the endosperm are a prolamin (gliadin) and a glutelin (glutenin). The mixture of proteins present in the endosperm is often referred to as 'gluten'. Wheat glutes vary in properties and it is mainly the properties of the gluten which decide whether the flour is suitable for bread or biscuit making. All glutes possess the property of elasticity. Strong glutes are preferred for bread making, and form a dough which traps the gases produced during yeast fermentation.

This property of gluten is considered to be the main reason why finely ground wheat is unpalatable when given in any quantity to animals. Wheat, especially if finely milled, forms a pasty mass in the mouth and this may lead to digestive upsets. Poultry are less susceptible, although wheat with a high gluten content should not be given since a doughy mass may accumulate in the crop. Newly harvested wheat is apparently more harmful in this respect than wheat which has been stored for some time.

Experiments have shown that it is unnecessary to grind or crush wheat for sheep, but the grain is best given coarsely ground or crushed for cattle.

Wheat By-products

The wheat grain consists of about 85 per cent. endosperm, 13 per cent. bran or seed coat and 2 per cent. germ. In modern flour milling the object is to separate the endosperm from the bran and germ. The wheat after careful cleaning and conditioning is blended into a suitable mix (grist) depending upon the type of flour required, and is passed through a series of rollers arranged in pairs. The first pair have a tearing action and release the bran coat from the endosperm. The rollers gradually break up the kernels, and at the end of the various stages the flour is removed by sieving. The proportion of flour obtained from the original grain, known as the extraction rate, varies, but in the United Kingdom is usually about 72 per cent. The remaining 28 per cent. constitutes the residues or 'offals' and can be classed into four main groups: wheat germ, bran, coarse middlings and fine middlings. In some mills the by-products are mixed and the combined product sold as 'all-in wheat feed'.

Wheat germ. Wheat germ is very rich in crude protein (22-32 per cent.) and low in fibre, and is an excellent source of thiamine and vitamin E. The wheat germ may be sold, after processing, for human consumption, although most of it is contained in the fine middlings.

Bran. The bran, which essentially comprises the husk of the grain

with some adhering endosperm, is graded according to size as 'giant', 'broad' or 'fine' bran, or the whole product sold as 'straight run bran'. These grades of bran are similar in composition, any variations depending mainly upon the composition of the grist, although giant bran is frequently higher in moisture content (up to 18 per cent) than the other grades, which generally contain about 12 per cent.

Bran is the most fibrous of the by-products and contains from 8.5 to 12 per cent crude fibre. The crude protein content ranges from 12.5 to 16 per cent according to variety of grain. The net energy value of bran is low, its popularity as a food for ruminant animals and horses being due to its well known physical properties. When made into a mash with warm water it acts as a laxative, but when given dry it tends to counteract scouring. Because of its fibrous nature and low digestibility bran is not commonly given to pigs and poultry.

Coarse middlings This by-product, sometimes known as common thirds, consists of small particles of bran together with part of the endosperm, and is of lower crude fibre content (6-8.5 per cent) and higher energy value than bran. The protein content ranges from 15 to 18 per cent, and the material is a more suitable food than bran for pigs and poultry. In common with other cereal by-products coarse middlings are deficient in calcium.

Fine middlings Fine middlings or fine thirds contain less bran particles than coarse middlings, and those present are in a pulverised form approaching flour particle size. Consequently the crude fibre content is low (usually 2-4 per cent) and the energy value relatively high, being similar to that of barley. The protein content is similar to that of coarse middlings, and the material is a valuable food for pigs and poultry.

MAIZE (*Zea mays*)

A number of different types of maize exist and the grain appears in a variety of colours, yellow, white or red. Yellow maize contains a pigment, cryptoxanthin, which is a precursor of vitamin A. In the U.S.A., where large amounts of this cereal are grown, the yellow varieties are preferred for animal feeding. The pigmented grain tends to colour the carcass fat, which in the United Kingdom is not considered desirable, so that white maize varieties are generally preferred here for feeding fattening animals.

Maize, like the other cereal grains, has certain limitations as a food for farm animals. Though an excellent source of digestible energy it is low in protein, and the proteins present are of poor quality. Maize

contains about 65 per cent. starch, is very low in fibre and has a high metabolisable energy value.

The crude protein content of maize is very variable and generally ranges from about 8 to 13 per cent., although varieties have been developed recently containing even higher amounts. In the U.S.A. the tendency has been to develop hybrid varieties of lower protein content.

The maize kernel consists of two main types of protein. Zein, occurring in the endosperm, is quantitatively the most important, but this protein is deficient in the essential amino acids, tryptophan and lysine. The other protein, maize glutelin, occurring in lesser amounts in the endosperm and also in the germ, is a better source of these two amino acids. The oil of maize (3-6 per cent.) contains a high proportion of unsaturated fatty acids and tends to produce a soft body fat. Maize is generally crushed or even roughly ground for feeding most farm animals.

Flaked maize. Flaked maize is prepared from maize by cooking with steam and passing through rollers, thus producing a thin flake which is then dried. Flaked maize is considered to be more acceptable to animals and is of slightly higher digestibility than the unprocessed grain. The heat treatment partly dextrinises the starch, and this affects the fermentation products obtained in the rumen. The feeding of dairy cows with flaked maize in relatively large amounts is known to depress the butterfat content of milk. This is considered to be due to a decrease in the proportion of acetic to propionic acids in the rumen.

Maize By-products

In the manufacture of starch and glucose from maize, a number of by-products are obtained which are suitable for feeding farm animals.

The ground grain is soaked in water and the germ floats to the surface, whence it is removed. The residue is ground and the bran is removed by sieving. The remaining liquid contains the endosperm, consisting mainly of starch and gluten. The starch is allowed to settle out, and the gluten, together with some fibrous material, passes on. The three by-products obtained are germ meal, bran and gluten meal. The germ is very rich in oil, most of which may be extracted before producing the germ meal.

These three products are frequently mixed together and sold as maize gluten feed. This product contains about 24 per cent. crude protein and only about 3.5 per cent. crude fibre. It is a valuable

concentrate food and is given to all classes of animals. Because of the poor quality of the protein, however, it should not form the main protein source in the diet of pigs and poultry.

RICE (*Oryza sativa*)

Rice, the main cereal crop of eastern and southern Asia, requires a sub-tropical or warm temperate climate and little is grown in Europe north of latitude 49°

Rice, when threshed, has a thick fibrous husk or hull like that of oats, and in this state is known as rough rice. The hull amounts to some 20 per cent of the total weight and is rich in silica. The hull is easily removed to leave a product known as brown rice. Brown rice is still invested in the bran, which may be removed with the aleurone layer and the germ by skinning and polishing, thus producing polished rice.

Rough rice may be used as a food for ruminants and horses, but brown rice is preferable for pigs and poultry and compares favourably with flaked maize in protein and energy value. Most rice, however, is used for human consumption and little is available in the United Kingdom for farm animals.

The two main by products obtained from rice milling are the hulls and rice meal. The hulls, apart from being very fibrous, have sharp edges which may irritate the intestine, and should never be given to animals. Rice meal or rice bran comprises the pericarp, the aleurone layer, the germ and some of the endosperm, and is a valuable product containing about 11-13 per cent crude protein and 10-15 per cent oil. The oil is particularly unsaturated and may become rancid very quickly, if it is removed a product of better keeping quality is obtained. The amounts of oil, crude protein and crude fibre must be declared in rice meal sold in the United Kingdom.

In the preparation of starch from rice, a product known as rice sludge or rice slump is left as a residue. The dried product has a crude protein content of about 26 per cent and low crude fibre and oil contents, and is suitable for ruminants and pigs.

RYE (*Secale cereale*)

The use of rye in the United Kingdom is relatively small and little is grown for feeding to farm animals. Rye grain is very similar to wheat in composition, but it is regarded as being the least palatable of the

cereal grains. It is also liable to cause digestive upsets and should always be given with care and in restricted amounts.

Rye contaminated with ergot may be dangerous to animals. This fungus contains a mixture of alkaloids which, if consumed by pregnant animals, may cause abortion. Like wheat, rye should be crushed or coarsely ground for feeding animals. Rye is not commonly given to poultry.

Most of the rye grown in the United Kingdom is used for the production of rye breads and speciality products for human consumption. Some is used for brewing and distilling. The offals from the production of rye malt are rye bran and rye malt culms, but these are available in such small amounts as to be of little importance.

MILLET

The name 'millet' is frequently applied to several species of cereals which produce small grains and are widely cultivated in the tropics and warm temperate regions of the world.

The most important members of this group include *Pennisetum typhoideum* (Pearl or Bulrush Millet), *Setaria italica* (Foxtail, Italian, Hungarian Millet), *Panicum miliaceum* (Proso-Millet or Broom Corn Millet) and *Echinochloa frumentacea* (Japanese Barnyard Millet or Sanwa Millet); all are members of the Paniceae tribe of grasses. Another millet, belonging to the tribe Chlorideae, is *Eleusine coracana* (Finger Millet or African Millet).

The crude protein content of millet may show considerable variation but is usually within the range 10-12 per cent.; the oil content is between 2 and 5 per cent. and the crude fibre between 5 and 9 per cent. Millet has a nutritive value very similar to that of oats, and contains a high percentage of indigestible fibre owing to the presence of hulls which are not removed by ordinary harvesting methods. Millet is a small seed and is usually ground for feeding to animals other than poultry.

SORGHUM (*Sorghum vulgare*)

Sorghum is the main food grain in Africa and parts of India and China. This cereal is also grown in the southern parts of the United States, as it is more drought-resistant than maize.

The kernel of sorghum is very similar to that of maize, although smaller in size. It generally contains rather more protein but less oil than maize.

FURTHER READING

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PROTEIN CONCENTRATES

OILSEED CAKES AND MEALS

Oilseed cakes and meals are the residues remaining after the removal of the greater part of the oil from oilseeds. Most of these are of tropical origin; they include groundnut, cottonseed, linseed and soya bean. The residues are rich in protein (20 to 50 per cent.) and most are valuable foods for farm animals. Some seeds, such as castor bean, yield residues unsuitable for animal feeding because they contain toxic substances.

Three main processes are used for removing oil from oilseeds. Two employ pressure to force out the oil, while the other uses an organic solvent, usually hexane but occasionally trichlorethylene, to dissolve the oil from the seed. Some seeds such as groundnut, cottonseed and sunflower have a thick coat or husk which is rich in fibre and of low digestibility and lowers the nutritive value of the material. It may be completely or partially removed by cracking and riddling, a process known as decortication. The effect of decortication of cottonseed upon the nutritive value of the cake derived from it is shown in Table 21.1; removal of the husk lowers the crude fibre content and has an important effect in improving the apparent digestibility of the other constituents. As a result the nutritive value of the decorticated cake is raised significantly above that of the undecorticated. The latter is only suitable for feeding adult ruminants, for whom it may have a role in maintaining the crude fibre level. Undecorticated cakes are rarely produced nowadays.

The seed from which oil is to be removed is cracked and crushed to produce flakes about 0.01 in. thick, which are cooked at temperatures up to 104° C for 15 to 20 minutes. The temperature is then raised to about 110 to 115° C until the moisture content is reduced to about 7 per cent. for the *hydraulic process*, or 3 per cent. for the *expeller process*. In hydraulic pressing the material is then made into cakes, wrapped in heavy cloth, and subjected to pressures of about 2000 lb per sq. in. for up to 60 minutes. The oil is thus expressed, and a hard

cake with an oil content of 7 to 8 per cent remains in the press. This is cracked and usually ground for feeding to animals, although cracked unground cakes may be given to ruminants. In the expeller process the material is passed through a perforated horizontal cylinder in which revolves a screw of variable pitch. Pressures up to 6000 lb per sq in are attained, and temperatures may be up to 30° C higher than in hydraulic pressing. The residue from screw pressing usually has an oil content of between 2½ and 4 per cent.

TABLE 21.1 Composition and Nutritive Value of Cottonseed Cakes

	Composition (per cent)					Ash
	Dry matter	Crude protein	Ether extract	N free extractives	Crude fibre	
Uncorticated	88	20.3	4.8	35.3	21.8	5.8
Decorticated	90	41.1	8.0	26.4	7.8	6.7

	Digestibility (per cent)				Digestible crude protein (per cent)	Starch equivalent
	Crude protein	Ether extract	N free extractives	Crude fibre		
Uncorticated	77	94	54	20	15.6	40
Decorticated	86	94	67	28	35.3	68

Only material with an oil content of less than 35 per cent is suitable for solvent extraction. If material of higher oil content is to be so treated, it first undergoes a modified screw pressing to lower the oil content to a suitable level. The first stage in solvent extraction is flaking, after this the solvent is allowed to percolate through the flakes, or a process of steeping may be used. The oil content of the residual material is usually below 1 per cent and it still contains some solvent, which is removed by heating. Some meals may benefit from being heated, and advantage is taken of the evaporation of the solvent to do this, soya bean meal, for example, is toasted at this stage in its production.

Some 95 per cent of the nitrogen in oilseed meals is present as true protein. It usually has a digestibility of 75 to 90 per cent, and is of good quality. When biological value is used as the criterion for judging protein quality, that of the oilseed proteins is considerably

higher than that of the cereals (Table 21.2). Some of them approach animal proteins like fish meal and meat meal in quality, though they are not as good as animal proteins as a class. Certainly they are of poorer quality than the better animal proteins such as those of milk and eggs. The figures for protein efficiency ratio and gross protein value confirm the good quality of oilseed proteins, but their chemical scores are low. This means that they have a badly balanced amino

TABLE 21.2. Nutritive Value of Some Food Proteins

<i>Source</i>	<i>Biological value (Rat)</i>	<i>Chemical score</i>	<i>Protein efficiency ratio (Rat)</i>	<i>Gross protein value (Chick)</i>
Oats	65	46		
Wheat	67	37		
Maize	55	28		
Cottonseed meal	80	37	2.0	77
Groundnut meal	58	24	1.7	48
Soya bean meal	75	49	2.3	79
White fish meal	77			102
Milk	85	69		90
Whole egg	95	100		

acid constitution, having a large deficit of at least one essential amino acid. In general, oilseed proteins have a low glutamic acid, cystine and methionine content, and a variable but usually low lysine content. As a result they cannot provide adequate supplementation of the cereal proteins with which they are commonly used, and should be used in conjunction with an animal protein when given to simple-stomached animals. The quality of the protein in a particular oilseed is relatively constant, but that of the cake or meal derived from it may vary, depending upon the conditions used for the removal of oil. The high temperatures and pressures of the expeller process may result in a lowering of digestibility and in denaturation of the protein, with a consequent lowering of its nutritive value. The less extreme conditions of the hydraulic process will yield a protein more like that of the original seed. Solvent extraction does not involve pressing, temperatures are comparatively low, and the protein of the meals is very similar to the original. In some cases the high temperatures and pressures of the expeller process may actually be beneficial, for example in the case of cottonseed where they inactivate gossypol.

The oilseed cakes may make a significant contribution to the energy content of the diet, particularly where the oil content is high. This will depend upon the process employed and its efficiency. Expeller soya

bean meal may have an oil content of 5.6 per cent and a starch equivalent of 69, compared with an oil content of 1.5 per cent and a starch equivalent of 64 for solvent extracted meal. Digestive disturbances, however, may result from uncontrolled use of cakes rich in oil, and if the oil is unsaturated, milk or body fat may be soft and carcass quality lowered.

The oilseed meals usually have a high phosphorus content, which tends to aggravate their generally low calcium content. They may provide useful amounts of the B-vitamins, but are poor sources of carotene and vitamin E.

Soya Bean Meal

Soya beans contain from 16 to 21 per cent of oil and are normally solvent-extracted, when a residual meal with an oil content of about 1 per cent is obtained. The meal is generally regarded as one of the best sources of protein available for animal feeding. The protein contains all the essential amino acids, but the amounts of cystine and methionine present are sub optimal. Methionine is the chief limiting amino acid, particularly in high energy diets.

Soya bean meal contains a number of toxic, stimulatory and inhibitory substances, including allergenic, goitrogenic and anticoagulant factors. Of particular importance in nutrition is a trypsin inhibitor which reduces the value of protein by reducing peptide digestion. The inhibitor may be inactivated by heating, which accounts for the preference shown for toasted meals in feeding simple stomached animals. For ruminant animals the inhibitor is not important and toasting is unnecessary. The process of toasting must be carefully controlled, since overheating will reduce the availability of lysine and arginine and reduce the value of the protein.

Provided the meal has been properly prepared, it forms a very valuable protein food for all farm animals. However, if soya bean meal is used as the major protein food for simple stomached animals, certain problems arise. The meal is a poor source of B vitamins, and these must be provided either as a supplement or in the form of an animal protein such as meat meal or fish meal. If such supplementation is not practised, sows may produce weak litters which grow slowly because of reduced milk yields, and older pigs show incoordination and failure to walk. On such diets breeding hens produce eggs of poor hatchability, giving chicks of poor quality, such chicks may also have an increased susceptibility to haemorrhages owing to a shortage of vitamin K. Soya bean meal is a better source of calcium and phosphorus than the

cereal grains, but where it replaces animal protein foods, adjustments must be made in the diet, particularly for rapidly growing animals and laying hens. Soya bean meal contains a substance, genistein, which has oestrogenic properties and a potency of 4.44×10^{-6} times that of diethylstilboestrol. The effect of this constituent on growth rate has not been elucidated.

Groundnut Meal

The seeds of the groundnut are borne in pods, usually in pairs or threes. The seeds contain 25 to 30 per cent. of crude protein and 35 to 60 per cent. of lipid material. The pod or husk is largely fibrous. Groundnut meal is now usually made from the kernels and only occasionally is the whole pod used as the source, when an undecorticated meal is produced. The most common method of extraction practised is screw pressing, giving a residual meal with 5 to 10 per cent. of oil. Lower oil levels can only be achieved by solvent extraction, but this has to be preceded by screw pressing to reduce the initially high oil content. The composition of the meal will depend upon the raw material and the method of extraction used.

The protein of groundnut meal has sub-optimal amounts of cystine and methionine, although the limiting amino acid is lysine. Where the meal is used in high-cereal diets, adequate supplementation with animal protein is necessary. This also ensures that the deficiencies of vitamin B₁₂ and calcium are made good. Such supplementation is particularly important in fast-growing animals such as pigs and poultry. The palatability of the meal for pigs is high, but it should not form more than 25 per cent. of the diet as it tends to produce a soft body fat and may have a troublesome laxative action. This also limits its use for lactating cows, for whom it otherwise forms an excellent and acceptable protein source. It has been reported that both a growth factor and an antitrypsin factor occur in groundnut meal, but these reports are not well authenticated.

In the past few years there have been several reports of certain groundnut meals proving toxic to young animals, particularly turkey poults and ducklings; calves and lambs have also been affected. Such meals have been shown to be badly affected by a mould *Aspergillus flavus*, which produces a material called aflatoxin. This is a complex of compounds varying in number from two to twelve, all characterised by being fluorescent. Aflatoxin is carcinogenic and affected animals show extensive liver damage. Adult animals are not badly affected, but a serious problem arises when affected meal is

given to lactating cows, and the toxic material is transmitted to the milk and so to the human diet. Aflatoxin has only been isolated from mould infested consignments.

Cottonseed Meal

The protein of cottonseed meal is of good quality, but has the common disadvantage of oil seed residues of having a low content of cystine, methionine and lysine. The calcium content is low, and as the calcium to phosphorus ratio is about 1:6 deficiencies of calcium may easily arise. It is a good though variable source of thiamine, but is a poor source of carotene.

Where cottonseed meal is used as a protein source for young, pregnant or nursing pigs, or young and laying poultry, it must be supplemented with fish meal or meat and bone meal to make good a shortage of essential amino acids and calcium. A supplement of vitamins A and D should also be provided. Pigs and poultry do not readily accept the meal, largely owing to its dry dusty nature. No such difficulty is encountered with lactating cows, but complications may arise where large amounts are given, since the milk fat tends to become hard and firm and butter made from such fat is often difficult to churn and tends to develop tallowy taints. Another factor to be considered in feeding with cottonseed meal is that it has a costive action, though this is not normally a problem and may indeed be beneficial in diets containing large amounts of laxative constituents.

Cotton seeds contain 0.03 to 0.2 per cent of a yellow pigment known as gossypol. This is an aromatic aldehyde which has anti-oxidant properties and is a polymerisation inhibitor. It has a profound effect on simple stomached animals, being toxic to them at low levels, for example at 0.016 per cent of the diet of young chicks. Cottonseed meal should not form more than 10 per cent of pig diets. Cottonseed meal may adversely affect the storage quality of eggs when given to poultry at levels of more than 5 to 10 per cent of the diet, the yolks of such eggs are often olive green and the albumens pink. It is usually recommended that meals for poultry feeding should contain less than 0.02 per cent of gossypol. Ruminants show no ill effects even when fed on large quantities of cottonseed meal. Considerable control of gossypol content is possible by heating, but this in turn leads to denaturation of the protein and a lowering of the nutritive value. Fortunately the shearing effect of the screw press in the expeller process is an efficient gossypol inactivator at temperatures which do not reduce protein quality.

Coconut Meal

The oil content of coconut meal varies from 2.5 to 6.6 per cent., the higher-oil meals being very useful in the preparation of high-energy diets. They have the disadvantage, however, of a susceptibility to develop rancidity in storage. The protein is low in lysine and histidine, and this, together with the generally high fibre content of about 12 per cent., limits the use of the meal for simple-stomached animals. It is usually recommended that it should form less than 25 per cent. of pig diets and less than 5 per cent. of poultry diets. Where low-fibre coconut meals are available for simple-stomached animals, they have to be supplemented with animal proteins to make good their amino acid deficiencies. Neither protein quality nor fibre content is limiting where ruminant animals are concerned, and for them coconut meal provides an acceptable and very useful protein supplement. In diets for dairy cows it is claimed to increase milk fat content, but there is little evidence to substantiate such claims. The milk fats produced on diets containing considerable amounts of coconut meal are firm and excellent for butter making.

Coconut meal has the valuable property of absorbing up to 50 per cent. of its own weight of molasses, and as a result is popular in compounding.

Palm Kernel Meal

This food has a comparatively low content of protein, which is however of high quality, the only limiting amino acid being methionine. The ratio of calcium to phosphorus is more favourable than in many other oilseed residues. The meal is dry and gritty, especially the solvent-extracted product, and is not readily eaten; it is therefore used in mixtures along with more acceptable foods. Attempts to use it mixed with molasses have not been successful. It is used chiefly for dairy cows, for whom it has a reputation for increasing the fat content of the milk. Palm kernel meal is often described as being balanced for milk production, but in fact contains too high a proportion of protein to energy.

Despite the high quality of the protein and the relatively satisfactory calcium and phosphorus balance, palm kernel meal is not used widely in pig and poultry diets. This is due partly to its unpalatability and partly to its high fibre content, about 15 per cent., which reduces its apparent digestibility for such animals. The highest level of palm kernel meal recommended in the diet of simple-stomached animals is about 20 per cent.

Linseed Meal

Linseed meal is unique among the oilseed residues in that it contains from 3 to 10 per cent of mucilage. This is almost completely indigestible by non ruminant animals, but can be broken down by the microbial population of the rumen. It is readily dispersible in water, forming a viscous slime. Immature linseed contains a small amount of a cyanogenetic glycoside, linamarin, and an associated enzyme, linase, which is capable of hydrolysing it with the evolution of hydrogen cyanide. Low temperature removal of oil may result in a meal in which unchanged linamarin and linase persist, such meals have proved toxic when given as a gruel. Normal processing conditions however destroy linase and most of the linamarin, and the resultant meals are quite safe. In the dry state, meal containing linase and linamarin is a safe food. The pH of the stomach contents of the pig is sufficiently low to inactivate linase. In ruminants the hydrogen cyanide formed by linase action is absorbed into the blood very slowly, and this, coupled with its rapid detoxication in the liver and excretion via the kidney and lungs, ensures that it never reaches toxic levels in the blood.

It has been reported that linseed meal has a protective action against selenium poisoning.

The protein of linseed meal is not of such good quality as that of soya bean or cottonseed meals, having a lower methionine and lysine content. Linseed meal has only a moderate calcium content but is rich in phosphorus, part of which is present as phytate. It is a useful source of thiamine, riboflavin, nicotinamide, pantothenic acid and choline.

Linseed meal has a very good reputation as a food for ruminant animals which is not easy to justify on the basis of its proximate analysis. Part of the reputation may be due to the mucilage being capable of absorbing large amounts of water, resulting in an increase in the bulk of linseed meal in the rumen, this may increase the retention time in the rumen and give a better opportunity for microbial digestion. The lubricating character of the mucilage also protects the gut wall against mechanical damage and, together with the bulkiness, regulates excretion preventing constipation without causing looseness. Linseed meal given to fattening animals results in rapid gains compared with other vegetable protein supplements making the same protein contribution, and cattle attain a very good sleek appearance, though the body fat may be soft. The meal is readily eaten by dairy cows but tends to produce a soft milk fat.

Linseed meal is an excellent protein food for pigs, provided it is given with an animal protein supplement to make good its deficiency of methionine, lysine and calcium. This is particularly important with diets containing large amounts of maize.

Linseed meal is not a satisfactory food for inclusion in poultry diets. Retardation of chick growth has been reported on diets containing 5 per cent. of linseed meal, and deaths in turkey poults at a 10 per cent. level. These adverse effects can be avoided by autoclaving the meal or by increasing the levels of vitamin B₆ in the diet. Some workers consider the adverse effects of the meal to be due to the mucilage, since this collects as a gummy mass on the beak, causing necrosis and malformation and reducing the bird's ability to eat. Pelleting or coarse granulation can overcome this trouble. If linseed meal has to be included in poultry diets the level should not exceed 3 per cent.

Other Oilseed Cakes and Meals

A number of other oilseed residues are used as foods for farm animals, including sunflower, sesame, kapok, niger and olive. Of these only sunflower and sesame are of any commercial importance. Decorticated sunflower meal is of fairly high protein content, about 38 per cent., but in spite of the absence of the seed coat the product is rich in fibre and is of low energy value.

Sesame meal is a high-protein concentrate containing about 46 per cent. crude protein, rich in arginine and leucine but low in lysine and methionine, and it may be used in feeding farm animals in much the same way as groundnut meal.

ANIMAL PROTEIN CONCENTRATES

These materials are given to animals in much smaller amounts than the oil seed derivatives so far discussed, since they are not used primarily as sources of protein *per se* but to make good deficiencies of certain essential amino acids from which non-ruminant animals may suffer when they are fed on all-vegetable protein diets. In addition they often make a significant contribution to the animals' mineral nutrition, as well as supplying various vitamins of the B-complex. A further reason why these products are given in limited quantities to farm animals is that they are expensive, which makes their large-scale use uneconomic.

Fish Meal

Two types of meals are recognised under British law. The first is fish meal, defined as

- a product obtained by drying and grinding or otherwise treating fish or waste of fish, to which no other matter has been added

The second is white fish meal, defined as

- a product (containing not more than 6 per cent oil and not more than 4 per cent salt) obtained by drying, grinding or otherwise treating white fish or waste of white fish, to which no other matter has been added

Although meals with an oil content of up to 10 per cent have been given successfully, it is generally considered that only meals complying with the second definition should be given to farm animals. The requirement of a maximum oil content was designed to prevent the inclusion of residues of high-oil fish such as the herring.

Fish meals are produced in two ways. The first is by steam drying, which may be either a batch process carried out under vacuum or a continuous process not employing reduced pressure. In both methods heating is carried out in steam jacketed vessels. In the flame drying process the meal is dried in a revolving drum by hot air from a furnace at one end of the drum. Flame drying is a more drastic process than steam drying and this may affect the quality of the protein, as illustrated in Table 21.3.

Commercially available fish meals are of fairly constant composition. They contain about 65 per cent crude protein, which may be of very good quality, as Table 21.3 shows. It is however variable, depending upon manufacturing techniques, its biological value for rats ranging from 36 to 82. Generally the protein has a high content of lysine, methionine and tryptophan and is valuable as a supplement in diets based mainly on cereal protein, particularly if this is derived from maize. Fish meals have a high mineral content, about 21 per cent, which is of value nutritionally since it contains a high proportion of calcium (8 per cent) and phosphorus (3.5 per cent) and also a number of desirable trace minerals including manganese, iron and iodine. They are a good source of vitamins of the B complex, particularly choline, B₁₂ and riboflavin, and have an enhanced nutritional value because of their content of growth factors known collectively as the Animal Protein Factor (APF).

Fish meals find their greatest use with simple stomached animals but can be very valuable for young ruminant animals. They are used mostly in diets for young animals, whose demand for protein and the

essential amino acids is particularly high and for whom in addition the growth-promoting effects of APF are valuable. Such diets may include up to 15 per cent. of fish meal. With older animals, who need less protein, the level of fish meal in the diet is brought down to about 5 per cent., and it may be eliminated entirely from diets for those in the last stages of fattening. This is partly for economic reasons, since the protein needs of such animals are small, and partly to remove any possibility of a fishy taint in the finished carcass. This possibility must also be carefully considered with animals producing milk and eggs, which are vulnerable to taint development. The chances of producing such a taint with white fish meal are remote, but when it is included in production and finishing rations it should be kept to below 5 per cent.

TABLE 21.3. Effect of Processing on the Nutritive Value of Fish Meals

	<i>Digestibility of protein (per cent.)</i>	<i>Biological value of protein (per cent.)</i>
Flame-dried	62	71
Steam-dried	73	77

of the diet. Since adult ruminants are able to obtain amino acids and B-vitamins by microbial synthesis in the rumen, the importance of fish meal in their diets is considerably less. It can still make a contribution to their mineral nutrition, and many authorities believe that ruminants do benefit from the APF that fish meal supplies. For these reasons it is sometimes included in rations for adult ruminants at up to 5 per cent. of the diet.

Whale Products

Whale solubles. Bones, meat and blubber are minced, cooked with live steam, and the oil is removed in a separator. The aqueous extract is then acidified and the coagulated protein separated by centrifuging. The supernatant liquid is concentrated to 50 per cent. volume, giving whale solubles. The product contains a considerable amount of hydrolysed protein, providing a well balanced range of amino acids. It is a good source of riboflavin. There have been reports that the solubles have an anti-biotin effect, but results of trials have been variable.

Whale solubles are spray-dried to give whale protein meal, which is an excellent protein source but whose hygroscopic nature makes it difficult to use in practice.

Whale meal This is the residue when lean whale meat is subjected to the procedure described above. It is an excellent protein source, being particularly rich in lysine and methionine. The composition of whale meals is variable, depending upon the amount of bone in the material for extraction. The protein content may vary from about 19 to 75 per cent and the respective ash contents would be about 65 and 4 per cent. The protein is of good quality, being similar to that of white fish meal, and is of high digestibility.

Meat Meal—Meat and Bone Meal

In the Fertilisers and Feeding Stuffs Regulations (1960), feeding meat meal is defined as

‘ the product containing not less than 55 per cent of protein and not more than 4 per cent of salt, obtained by drying and grinding animal carcasses or portions thereof (excluding hoof and horn) to which no other matter has been added, but which may have been preliminarily treated for the removal of fat ’

Feeding meat and bone meal is defined as

‘ the product containing not less than 40 per cent of protein and not more than 4 per cent of salt, obtained by drying and grinding animal carcasses or portions thereof (excluding hoof and horn) and bone, to which no other matter has been added, but which may have been treated for the removal of fat ’

The meals may be produced by dry rendering, in which the material is heated in steam jacketed cookers and the fat which separates from the dehydrated product is allowed to drain away. More fat is removed under pressure, and the residue is ground to give the final product. In the wet rendering process the material is heated by live steam after water has been added. Fat separates and is skimmed off, the residue is allowed to settle and the supernatant liquor is drained off. This is known as ‘stuck’ and contains a considerable amount of protein. The residue is pressed to remove fat, dried and ground.

Meat meal generally contains from 60 to 70 per cent of protein compared with about 45 to 55 per cent for meat and bone meal. The fat content is variable, ranging from 3 to 13 per cent, but is normally about 9 per cent. Meat and bone meal contains more ash than meat meal and is an excellent source of calcium, phosphorus and manganese. Both meals are good sources of vitamins of the B complex, especially riboflavin, choline, nicotinamide and B₁₂. The protein of these meat by products is of good quality (BV approximately 67 for adult Man) and is particularly useful as a lysine supplement. Unfortunately it is a poor source of methionine and tryptophan. Various unidentified beneficial factors have been claimed to be present in meat meals,

among them the enteric growth factor from the intestinal tract of swine, the *Ackerman* factor and a growth factor located in the ash.

Meat products are more valuable for simple-stomached than for ruminant animals, since the latter do not require a supply of high-quality protein. The low methionine and tryptophan levels of the meals affect their value, however, because they cannot adequately make good the deficiencies of these amino acids in the high-cereal diets of pigs and poultry. This is particularly so where high proportions of maize are given, maize being particularly low in tryptophan. Usually meat meal is given in conjunction with another animal protein or with a vegetable protein to make good its low content of methionine and tryptophan. Both meat meal and meat and bone meal are eaten readily by pigs and poultry, and may be given at levels of up to 15 per cent. of the diet for laying hens and young pigs; for fattening pigs the level is usually kept below 10 per cent. As well as being less beneficial to ruminant than to simple-stomached animals, these products are not readily acceptable to ruminants and must be introduced into their diets gradually. Considerable care is required in storing the meat products to prevent the development of rancidity and loss of vitamin potency.

Feeding Dried Blood

Feeding dried blood is defined in the Fertilisers and Feeding Stuffs Regulations (1960) as

'... blood which has been dried, to which no other matter has been added'.

It is manufactured by passing live steam through the blood until the temperature reaches 100° C. This ensures efficient sterilisation and causes the blood to clot. It is then drained, pressed to express occluded serum, dried by steam heating and ground.

Feeding dried blood is a dark chocolate-coloured powder with a characteristic smell. It contains about 80 per cent. of protein, small amounts of ash and oil and about 10 per cent. of water, and is important nutritionally only as a source of protein. This is of poor quality, having a low digestibility and a low content of isoleucine and methionine and only a trace of glycine. The amino acid constitution is badly balanced, and the product has a low biological value.

Supplies of blood meal are very limited and expensive, so that the material is used chiefly in diets for young animals, mainly pigs. Where it forms more than 10 per cent. of the diet it tends to cause scouring. If blood meal is used to replace fish meal, care must be taken to provide adequate calcium and phosphorus as well.

Milk Products

Whole milk contains about 87.5 per cent of water and 12.5 per cent of dry matter, usually referred to as the total solids. Of this about 3.75 per cent is fat, the remainder forming the solids not fat (SNF) consisting of protein (3.3 per cent), lactose (4.7 per cent) and ash (0.75 per cent).

Most of the fat is neutral triglyceride having a characteristically high proportion of fatty acids of low molecular weight and forming an excellent source of energy. It has about $2\frac{1}{2}$ times the calorific value of the milk sugar or lactose. The crude protein fraction of milk is complex, about 5 per cent of the nitrogen being non-protein. Casein, the chief milk protein, contains about 78 per cent of the total nitrogen, and is of excellent quality but has a slight deficiency of the sulphur-containing amino acids, cystine and methionine. Fortunately the β lactoglobulin is rich in these acids, so that the combined milk proteins have a biological value of about 85. The most economic use of the protein is to supplement poor quality proteins like those of the cereals, for which purpose it is better than either the meat or fish products. Where however milk products are used to replace fish meal or meat and bone meal, the diet must be supplemented with inorganic elements, particularly calcium and phosphorus, since the ash content of milk is so low. Milk has a low magnesium content and is seriously deficient in iron. Normally milk is a good source of vitamin A but poor in vitamins D and E. It is a good source of thiamine and riboflavin and contains small amounts of vitamin B₁₂.

Whole milk is too valuable as a human food to be used for farm animals, except for young dairy and bull calves, and animals being prepared for competition. Two milk by-products are widely used, however, and are valuable foods for farm animals.

Skim milk This is the residue after the cream has been separated from milk by centrifugal force. The fat content is very low, below 1 per cent, and the value of the by-product as a source of energy is much reduced, about 162 kcal/lb as compared with 340 kcal/lb for whole milk. Removal of the fat in the cream also means that skim milk has little or none of the fat-soluble vitamins. However, it does result in a concentration of the SNF constituents. Skim milk finds its main use as a protein supplement in the diets of simple-stomached animals and is rarely used for ruminant animals; it is particularly effective in making good the amino acid deficiencies of the largely cereal diets of young pigs and poultry. For pigs it is usually given in the liquid state, and limited to a *per capita* consumption of 5 to 6 pints per day.

Where the price is suitable it may be given *ad lib*, and up to 5 gallons per pig per day may be consumed along with about 2 lb of meal. Scouring may occur at these levels but can be avoided with reasonable care. Liquid skim milk must always be given in the same state, either fresh or sour, if digestive troubles are to be avoided. It may be preserved by adding $1\frac{1}{2}$ gallons of formalin to 1000 gallons of skim milk. For feeding poultry, skim milk is normally used as a powder, and may form up to 15 per cent of the diet. It contains about 35 per cent of protein, the quality of which varies according to the manufacturing process used. roller-dried skim milk is subjected to a higher drying temperature than the spray-dried product and has a lower digestibility and biological value (Table 21.4). For poultry skim milk protein has the disadvantage of a low cystine content.

TABLE 21.4 Effect of Processing on the Nutritive Value of Skim Milk

	<i>Digestibility of protein (per cent)</i>	<i>Biological value of protein (per cent)</i>
Spray dried	96	89
Roller-dried	92	82

Whey. When milk is treated with rennet in the process of cheese-making, casein is precipitated and carries down with it most of the fat and about half the calcium and phosphorus. The remaining serum is known as whey, which as a result of the partition of the milk constituents in the rennet coagulation is a poor source of energy (123 kcal/lb), fat soluble vitamins, calcium and phosphorus. Quantitatively it is a poorer source of protein than milk, but most of the protein is β -lactoglobulin and of very good quality. Whey is usually given *ad lib* to pigs in the liquid state. Dried whey is rarely used, as it is intensely hygroscopic and difficult to maintain in a satisfactory physical condition.

FURTHER READING

- A. M. ALTSCHUL, 1958 *Processed Plant Protein Foodstuffs* Academic Press, New York
 F. B. MORRISON, 1959 *Feeds and Feeding* Morrison Publishing Co., Iowa
 B. H. SCHNEIDER, 1947 *Feeds of the World, their Digestibility and Composition* Agric. Exp. Sta. West Virginia University, U.S.A.

GROWTH-STIMULATING SUBSTANCES

ANTIBIOTICS

Antibiotics may be defined as chemical substances, produced by micro-organisms, which in dilute solution have the capacity of inhibiting the growth of other micro-organisms, and even of destroying them. They were originally developed for medical and veterinary purposes to control specific pathogenic organisms, but in 1949 it was discovered that certain antibiotics could increase the rate of growth of young pigs and chicks when included in their diet in small amounts. The growth-promoting properties of these compounds were at first thought to be due to the presence of vitamin B₁₂ in the antibiotic preparations, but it was later shown that the antibiotic gave greater growth responses than the pure vitamin.

In the United Kingdom the Therapeutic Substances Act forbids the use of many antibiotics as animal feed supplements. Penicillin, oxytetracycline and chlortetracycline may be used in animal feeding stuffs or in supplements intended for incorporation in feeding stuffs mixed on the farm, but the materials must not contain more than specified quantities of antibiotic, and they must be sold under an approved label, which currently states*

** In no circumstances should this ration be fed to adult breeding stock, laying poultry or ruminants except under the direction of the veterinary surgeon or practitioner in attendance **

Apart from the three antibiotics in current use as feed additives, others such as bacitracin, streptomycin, tyrothricin, gramicidin, neomycin, olcandomycin and erythromycin have given growth responses in the feeding of young animals.

Antibiotics may be classified into 'broad-spectrum' antibiotics such as the tetracyclines, and 'narrow-spectrum' antibiotics such as penicillin, streptomycin and bacitracin. The former are inhibitory to a much wider range of bacteria than the narrow-spectrum antibiotics.

Antibiotics in Pig Feeding

The optimum level for most antibiotics in the diet is thought to be within the range 5–15 g per ton, and there is no advantage in exceeding these low levels

The response to antibiotics as growth stimulants in pig feeding is very variable, but growth rate increases of from 10 to 15 per cent with increases of 3 to 5 per cent in the efficiency of feed utilisation may be expected. Generally, the higher the standards of hygiene and general management, the lower the response. The best results are obtained

TABLE 22.1 The Effect on Liveweight Gain of adding Antibiotics to Two different Types of Diet given to Pigs from Weaning to Bacon Weight
(From *Antibiotics in Pig Food* A R C Report Series No 13, 1953
H M S O)

	<i>Animal protein diet *</i>			<i>Vegetable protein diet</i>		
	<i>Control</i>	<i>Pent- icillin</i>	<i>Chlortetra- cycline</i>	<i>Control</i>	<i>Pent- icillin</i>	<i>Chlortetra- cycline</i>
<i>Liveweight increase</i>						
<i>lb/day</i>	1 17	1 29	1 28	1 05	1 18	1 22
<i>Gain over control as percentage of control</i>	—	10 3	9 4	—	12 4	16 2

* Containing 10 per cent fish meal

with young fast growing animals of from 40 to 100 lb liveweight, thereafter the effect diminishes with age. In spite of the poorer response in mature animals it is usually recommended to continue giving antibiotics to animals throughout the fattening period, since abrupt withdrawal from the diet can cause a setback and nullify any initial advantage as a growth stimulant.

The response to antibiotics is greater with animals given all-vegetable protein diets than with those receiving animal protein supplements. The latter type of diet containing an antibiotic, however, still gives faster growth rates than those obtained on all-vegetable protein and antibiotic mixtures. Table 22.1 summarises the results of feeding trials carried out by the Agricultural Research Council at a number of centres and illustrates these points.

In practical pig feeding the antibiotics oxytetracycline or chlortetracycline are normally used, since these have been found more effective than penicillin for this species. Early research indicated that there did not appear to be any benefit from adding combinations of antibiotics to diets, but recently it has been reported from the U.S.A. that

the pattern is changing and that a combination of broad and narrow spectrum antibiotics improves weight gain and feed efficiency more than a single antibiotic

Antibiotics have been added to the diets of sucking pigs with some success, although the results are extremely variable. They have also been included in liquid sow milk substitutes and early weaning dry diets for young pigs with success, the main effect probably resulting from the control of ailments such as scours. There is some evidence, however, that antibiotics eventually become ineffective against bacteria responsible for scours in young pigs. Feeding pigs with antibiotics has little influence on carcass quality, although slightly fatter carcasses may be produced.

Antibiotics in Poultry Feeding

As with pigs, the degree of growth stimulation in poultry varies with the environment. Under hygienic conditions growth increases are small. In 'old' (infected) buildings increases of 10 per cent in the growth rate of fowls are likely to be obtained with similar increases in efficiency of feed utilisation.

The type and quantity of antibiotic given is important, and under certain conditions as little as 0.2 ppm of penicillin in the diet of chicks can increase the growth rate. When newly hatched chicks are given diets containing antibiotics the growth stimulating effect is noticeable within a few days and is most marked at the end of the first or second week. As with pigs, the effect diminishes with age.

Turkey poults give even greater responses to antibiotic supplementation than chicks, and increases of 15 per cent in the growth rate have been reported. Antibiotics are widely used by the poultry industry, particularly in broiler production. Besides the tetracyclines and penicillin, many newer types of antibiotic have been tested for their growth promoting properties with poultry, among the more recent, zinc bacitracin and oleandomycin have given promising results. Zinc bacitracin at levels of 5 g per ton has given a similar response to that of penicillin, and has improved egg production in laying hens. Table 22.2 compares the effectiveness of some of these antibiotics in stimulating the growth of young chicks.

Antibiotics in the Diet of Ruminant Animals

The effect of antibiotics on ruminants might be expected to be different from that on simple stomached animals, since ruminants depend primarily on bacterial growth for proper nutrition. As far

as mature ruminant animals are concerned, the results are conflicting. It has been suggested that the inclusion of antibiotics in the diet could be harmful by suppressing the activity of cellulolytic organisms and thus impairing cellulose digestion. On the other hand there is some evidence that, on low-roughage diets, antibiotics may have a beneficial effect on voluntary intake, on protein metabolism when the protein content is limiting, and on the digestion of starch. It is possible that antibiotics

TABLE 22.2. Comparison of the Effects of different Antibiotics on the Growth of Chicks to 8 Weeks of Age *
(From H. S. Goldberg (ed.), 1959, *Antibiotics, their Chemistry and Non-medical Uses*, p. 189. Van Nostrand, New York)

<i>Antibiotic †</i>	<i>All plant protein</i>	<i>Plant protein + 2 per cent. fish meal</i>
(None)	(100)	(100)
Streptomycin	107	102
Oxytetracycline	111	105
Chlortetracycline	111	107
Bacitracin	112	111
Procaine penicillin	116	110

* Nine ppm of antibiotic in the feed.

† The values are relative weights, the weight of birds given no antibiotic being set arbitrarily at 100.

may have some value when added to rations composed mainly of concentrates, such as those used in 'barley beef' production, although more information is required. From results of present investigations it would seem unwise to recommend including antibiotics in diets with a normal fibre content.

The ruminants most likely to benefit from antibiotics are young calves, in whom both oxytetracycline and chlortetracycline are effective in improving growth and in reducing the incidence and severity of scours. These two antibiotics increase feed consumption and result in increases in growth rates of from 5 to 25 per cent. Most of the growth improvement occurs before the animals are 8 weeks old. The narrow-spectrum antibiotic, penicillin, is less effective than the tetracyclines. The inclusion of antibiotics in the rations of calves is probably justified by the beneficial effects in combating calf scours, any growth advantage in the early life of the animal becoming insignificant in the mature ruminant.

Mode of Action of Antibiotics

The exact method by which antibiotics exert their growth-stimulating

effect is not known, although many theories have been proposed. It is likely that there is no single explanation and that antibiotics have several modes of action.

Part of the growth promoting action of antibiotics may result from their therapeutic effects, and it has been suggested that they (1) reduce or eliminate the activity of pathogens causing 'subclinical infection', (2) eliminate bacteria which produce toxins that reduce the growth potential of the animal, (3) stimulate the growth of micro organisms that synthesise known or unidentified nutrients, (4) reduce the growth of micro organisms that compete with the host for supplies of nutrients.

There is considerable evidence to support the subclinical infection theory, since germ free chicks, or birds reared in a new, clean environment, grow better than chicks in 'infected' buildings, and whereas chicks housed in the latter respond well to antibiotic supplementation, those in the former show little response.

The use of antibiotics leads to a reduced requirement for vitamin B₁₂ and an increased conversion of food nitrogen into body nitrogen, which could partly explain the greater response with vegetable protein diets than with mixed diets containing animal protein. In calves, growth promoting effects can sometimes be attributed entirely to increased food intake.

Potential Hazards in the Use of Antibiotics

The use of antibiotics for controlling disease in Man has been complicated by the development of resistant strains of organisms. It has been suggested that the continued use of antibiotics as feed supplements may encourage the development of resistant bacteria, either in the animal itself or in human beings consuming meat and products that contain antibiotic residues. As far as the animal is concerned, there is evidence that the routine administration of antibiotics to pigs causes the development of antibiotic resistant strains of *Escherichia coli* an organism which is thought to be associated with scours in young pigs.

With regard to the human health hazard, chlortetracycline is not detectable in the serum or tissues of farm animals when given in amounts of 10 to 20 ppm of the diet. At levels of 1000 ppm of the diet this antibiotic has been recovered from tissue in quantities of the order of 100 ppm of tissue. These trace quantities of antibiotic resulting from such massive dosage rapidly disappeared from the tissues when the antibiotic was withdrawn from the diet one or two days before slaughter or else when the meat was cooked.

It seems safe to conclude from the foregoing that the prolonged use of antibiotics for farm animals at the normal recommended levels is unlikely to cause any public health hazard.

HORMONES

Natural hormones are specific chemical substances produced by living cells. They are normally passed into the blood stream and transported to organs and tissues to modify their structure and function. Hormones have the property of being effective when present in extremely small amounts. Some synthetic compounds such as diethylstilboestrol (commonly known as stilboestrol), hexoestrol and dienoestrol, which do not occur in nature, have hormone-like properties.

Of particular interest in nutrition are the growth-promoting properties of certain hormones. Oestrogens, androgens, progestogens and the pituitary growth hormone are all known to stimulate growth. In addition thyroxine can stimulate growth, wool production and milk yield under certain conditions. Iodinated casein is a commercial product which has an activity several times greater than that of dried thyroid gland. Results of experiments in which iodinated proteins have been given in the diet to cows have been variable, although if the hormone-containing compound is administered over a short period at the right stage of lactation, milk yield may be increased. Thyroproteins have also been used for increasing wool growth. It is doubtful however if iodinated proteins are likely to be of practical value in animal production.

The use of the synthetic oestrogenic hormones, stilboestrol and hexoestrol, has attracted more attention in recent years, and these are in commercial use as growth promoters in many countries, including the United Kingdom.

Synthetic oestrogens may be administered to farm animals orally or by subcutaneous implantation. For the latter process pellets are usually placed at the base of the ear in ruminants, and in the neck in the chemical caponisation of cockerels; these sites are chosen so that the pellets are discarded and not consumed by human beings. Treated poultry become docile, and fat accumulates in the body cavity, under the skin and within the muscles. The administration of oestrogenic compounds to broilers during the last 4-6 weeks of the growing period has been reported to give an improved rate of gain, a better carcass appearance, and in some cases better feed efficiency.

The widest application of the use of synthetic oestrogenic hormones

has undoubtedly been in the field of beef cattle and fat lamb production. The effect of the administration of hormones to ruminants is different from that observed in poultry, in that for ruminants smaller amounts are used relative to their size, and that, instead of increased fat deposition, carcasses from treated animals contain more muscle, more bone and less fat than carcasses from untreated animals.

It is thought that the hormone alters the metabolism so as to increase muscle and bone formation at the expense of fat deposition. Since the energy required to synthesise protein or bone is less than that required to synthesise the same weight of fat, and the amount of water in muscle is greater than in body fat, it follows that a given amount of food will produce a higher liveweight increase in a hormone treated than in an untreated animal.

Hexoestrol is the hormone normally used in commercial fattening in the United Kingdom, the method of administration most favoured being implantation. The optimum implant for beef cattle is from 45 to 75 mg, when hexoestrol is mixed with the food 10 mg per day is the recommended dose. The corresponding levels for sheep are 10 to 15 mg by implantation or 2 to 4 mg daily in the food. The best results are obtained with animals in the later stages of growth on a high plane of nutrition. The degree of response varies, up to 60 per cent increase in weight gain has been reported for beef cattle, although an average figure is probably about 25 per cent. Treatment does not increase the amount of food consumed appreciably.

Table 22.3 shows the results of an experiment carried out at the Rowett Research Institute with 36 wether lambs divided into three groups. One group was slaughtered and analysed in order to determine the initial body composition of the lambs. The second group was implanted with hexoestrol (15 mg/animal), while the third group was not treated. The last two groups were fattened for about 90 days and then slaughtered and analysed.

The results in Table 22.3 show that the hormone treated lambs gained in liveweight 27 per cent faster than the untreated animals, and laid down more protein, water and bone but less fat than the untreated lambs.

Potential Hazards in the Use of Hormones

A potential risk in the use of synthetic oestrogens is the development of 'side effects' in the treated animals. These consist of undue restlessness, development of high tail heads and milk secretion from rudimentary teats. These side effects are more liable to occur if excessive

amounts of hormones are used. A more serious criticism is the human health hazard arising from the possible carcinogenic properties of residues of the synthetic oestrogens in the carcass. In the U.S.A. the use of stilboestrol for chemical castration of poultry was made illegal because minute residues of the hormone had been shown to be present in the liver, skin and kidneys of treated birds. In the U.S.A.

TABLE 22.3 The Effect of Hexoestrol Implantation on the Growth of Lambs over a 90 Day Period

(From T. R. Preston, Isoline Gee, and J. A. Crichton, 1957, *Agric. Rev.* 3, 39)

(1) *Increases in the liveweight and certain constituents of the carcass of lambs during fattening*

<i>Increase in</i>	<i>Hexoestrol group (lb)</i>	<i>Control group (lb)</i>	<i>Effect of hexoestrol (per cent)</i>
Liveweight	52.0	41.0	+27
Fat	10.7	11.4	-6
Protein	2.9	2.1	+38
Water	10.6	7.0	+51
Bone	2.3	1.0	+130

(2) *Efficiency of food utilisation*

	<i>Hexoestrol group</i>	<i>Control group</i>
Increase in liveweight per unit of organic matter consumed (lb/lb)	0.236	0.191
Increase in protein in edible meat per unit of protein consumed (lb/lb)	0.076	0.058
Increase in energy in edible meat per unit of organic matter consumed (Mcal/lb)	0.539	0.580

stilboestrol may be used for fattening beef cattle and sheep, but its use is governed by strict regulations on levels and feeding rates, and is subject to the condition that no residue of the hormone shall be present in any edible portion of the treated animal after slaughter.

A further criticism of the continued use of hormones is the possible contamination of pastures through the excreta from hormone-treated animals. This risk could be particularly great for breeding animals subsequently grazing these pastures, who should never be given synthetic oestrogens.

The whole question whether hormones should be used as growth promoters is still debatable, but it seems logical that with any feeding system the economic advantages, however great, should never take precedence over any potential risk to human health.

OTHER GROWTH STIMULATING SUBSTANCES

Arsenicals Arsenic compounds have long been used in veterinary medicine as 'tonics' to improve the general well-being and appearance of animals. In 1949 it was reported that organic arsenicals had growth-promoting properties similar to those of antibiotics when added to the diets of chicks. Compounds found to have this action included arsanilic acid, sodium arsanilate, arsonic acid (3 nitro-4-hydroxy-phenylarsonic acid) and arsenobenzene.

Although the exact mode of action of these compounds in increasing the growth rate is unknown, it seems likely that the beneficial effects result from their action on the intestinal microflora. Considerable care is required in administering arsenicals to animals, since arsenic is a cumulative poison and there is always a danger that those consuming meat from treated animals will be harmed.

Copper sulphate It has been demonstrated in experiments carried out at several research centres that copper sulphate added to a normal fattening diet of pigs at a level of 0.1 per cent of the diet (equivalent to about 250 ppm added copper) improves the rate of gain and feed conversion efficiency between weaning and bacon weight. Since this level of copper is far in excess of that regarded as satisfactory for normal growth, the beneficial effects of copper sulphate at this high level do not appear to be concerned with meeting a particular nutritional requirement for this element. Although copper sulphate has been, and is still, included in many commercial pig diets, its use has been widely criticised. Copper is a cumulative poison, and the livers of pigs fed on diets supplemented with copper sulphate may contain up to 20 times the concentration present in livers of untreated animals. It has been pointed out, however, that the copper content of pigs' liver is usually very much lower than that of other farm animals, and even when increased twentyfold the liver copper of the pig is only three times the normal copper content of calves' liver.

A further possible danger is introduced by the difficulty of ensuring adequate mixing of the copper salt in the ration. This is particularly important because the safety margin is low. It is known that 500 ppm of copper, i.e. double the recommended dose, is definitely toxic to pigs. Sheep are particularly susceptible to copper poisoning and there are several recorded cases of deaths through sheep eating copper fortified pig meals.

Tranquillisers These compounds are normally used medicinally for reducing hypertension and nervousness. Certain tranquilisers such

as the natural alkaloid of *Rauwolfia*, reserpine, and hydroxyzine have been shown in certain trials to improve daily liveweight gain when given to fattening bullocks. In other experiments the response has been nil, so that opinion is divided about their beneficial effects as growth promoters. Chlorpromazine and reserpine have been used to reduce excitability in fowls. It is possible that, where beneficial effects of tranquillisers as growth promoters do occur, these result from their action on the central nervous system protecting the animal against environmental stress.

Surfactants (detergents). It was reported in 1951 that certain surfactants had growth-promoting properties. Subsequent experiments have given contradictory results, and where responses have occurred these have not been as great as the responses from antibiotics.

FURTHER READING

- M. WOODBINE (ed.), 1962. *Antibiotics in Agriculture*. Butterworth, London.
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C. A. LASSITER, 1955. Antibiotics for Dairy Cattle. A Review. *J. Dairy Sci.*, 38, 1102-1138.
Antibiotics in Pig Food. Agricultural Research Council Report Series No. 13, 1953. H.M.S.O., London.
R. BRAUDE, S. K. KON AND J. W. G. PORTER, 1953. Antibiotics in Nutrition. A Review. *Nutr. Abstr. Rev.*, 23, 473-496.
Hormonal Relationships and Applications in the Production of Meats, Milk and Eggs, 1959. National Academy of Sciences—National Research Council Publ. No. 714. Washington, D.C.

APPENDIX

NOTE ON THE USE OF THE TABLES

The data given in these Tables have been compiled from a number of sources, a full list of which is given at the end of the Appendix. *Absence of figures does not imply a zero*, but merely that the information was not given in these sources.

Composition Tables 1-6

The composition of a particular food is variable, and figures given in these Tables should be regarded only as representative examples and not constant values.

The proportions of major constituents have been expressed as percentages. For trace nutrients, the unit 'parts per million' (ppm) has been preferred to mg/lb. The unit ppm is equivalent to mg/kg, and since 1 U.K. ton equals 1,016,047 g, for practical purposes ppm can be regarded as being equivalent to g/ton.

In Table 1, metabolisable energy (ME) values are given in addition to starch equivalent (SE) figures. The ME values have been calculated from total digestible nutrients (TDN) on the assumption that 1 lb of TDN supplies 1616 kcal ME for ruminants.

In Table 2, digestible energy (DE) values have been calculated from TDN, obtained from digestibility trials with pigs, on the assumption that 1 lb TDN has 2000 kcal of DE.

In Table 3, most of the values for poultry foods are abstracted from M.A.F.F. Bulletin No. 174 (Reference No. 3), and for a description of the method of calculating the ME values the reader is referred to this publication.

Nutrient Requirements Tables 7-11

The scientific rationing of farm animals is based on standards expressed in terms of either 'nutrient requirements' or 'nutrient allowances'. These terms are defined in Chapter 14. The figures in these Tables are expressed as nutrient requirements, with the exception of the energy and protein standards for ruminants, which are allowances since they include margins of safety for variation between animals.

As far as mineral and vitamin requirements are concerned, the

standards should be regarded as the minimum amounts which should be supplied to the animal.

BRITISH-METRIC EQUIVALENTS

One oz	= 28.349 g
One lb	= 453.6 g
One cwt	= 50.8 kg
One ton	= 1016 kg
One kg	= 2.205 lb

TABLE 1 NUTRITIVE VALUE OF FOODS FOR RUMINANTS

Food	Fresh basis					Dry matter basis		
	Dry matter, per cent	Crude protein, per cent	Crude fibre, per cent	Ether extract, per cent	Ash, per cent	Digestible crude protein, per cent	Starch equivalent	Metabolisable energy, kcal/lb
<i>Pasture grass</i>								
Very leafy	18	4.0	3.6	0.6	2.3	3.3	10.8	210
Leafy	19	3.3	4.5	0.5	2.2	2.5	11.3	220
Early flowering	21	3.0	5.4	0.7	2.1	2.1	12.2	240
Flowering	23	2.4	6.2	0.5	2.2	1.6	12.7	245
Seed set	25	2.1	7.4	0.6	1.8	1.3	12.8	260
<i>Green legumes</i>								
Red clover, early flowering	19	3.4	5.2	0.7	1.6	2.5	10.2	206
White clover, early flowering	19	4.4	4.3	0.8	2.1	2.8	8.8	180
White clover, bud stage	22	4.5	6.2	0.5	1.8	3.6	11.3	221
Lucerne, early flowering	24	4.1	7.2	0.4	2.4	3.1	10.3	210
Peas, early flowering	17	3.5	5.9	0.6	1.2	2.4	6.8	160
Sainfoin, early flowering	23	4.4	4.7	0.6	1.4	3.2	13.1	245
Vetches, in flower	18	3.2	5.1	0.5	1.5	2.2	7.5	165
<i>Other green crops</i>								
Cabbage (drumhead)	11	1.5	2.0	0.4	1.2	1.1	6.6	121
Cabbage (open leaved)	15	2.5	2.4	0.7	1.6	1.8	9.5	175
Kale (marrow stem)	14	2.2	2.5	0.5	1.9	1.7	9.1	161
Kale (thousand headed)	16	2.2	3.2	0.4	1.7	1.7	10.0	185
Maize	19	1.7	5.6	0.5	1.2	1.0	9.1	185
Oats	23	1.9	8.5	0.6	1.8	1.4	10.0	220
Rape	14	2.8	3.5	0.8	1.3	2.0	6.9	145
Sugar beet tops	16	2.0	1.6	0.5	3.4	1.4	8.6	166
Swede tops	12	2.3	1.5	0.5	2.2	1.6	5.5	115

†

TABLE I continued

<i>Silages</i>									
Grass, leafy	20	35	50	10	18	28	124	245	140
Grass, early flower	25	32	70	09	23	21	145	290	84
Grass, full flower	25	29	79	07	27	15	114	240	60
Lucerne	17	37	50	14	21	25	70	155	147
Maize	20	22	47	12	12	14	121	235	70
Oats	25	20	90	08	19	12	94	219	48
Potato, steamed	25	24	08	03	23	15	186	310	60
<i>Hay</i>									
Clover, very good	85	156	226	33	71	109	43	870	128
Meadow, leafy	85	137	195	30	78	93	49	896	109
Meadow, early flowering	85	100	266	16	68	54	41	820	64
Meadow, flowering stage	85	76	287	15	64	34	36	765	40
Meadow, seed set	85	48	306	12	53	24	33	745	28
Oat, milk stage	85	80	274	26	67	43	33	720	51
<i>Dried grass</i>									
Grass, very leafy	90	187	177	30	100	141	54	988	157
Grass, leafy	90	150	209	26	108	100	52	966	111
Grass, early flower	90	121	244	22	90	73	51	970	81
Lucerne, early flower	90	160	242	24	101	115	44	835	128
<i>Straws and chaff</i>									
Barley	86	33	339	18	46	08	23	691	09
Barley (high fibre)	86	24	401	15	36	-07	16	640	-08
Oat	86	29	339	19	49	10	20	644	12
Rye	86	32	369	16	26	06	15	595	07
Wheat	86	29	359	13	61	01	13	545	01
Bean	86	45	431	08	46	22	19	710	26
Pea	86	90	353	16	66	43	17	610	50
Oat chaff	86	60	228	21	103	22	29	590	26

Continued overleaf

ANIMAL NUTRITION

Food	Dry matter, per cent	Crude protein, per cent	Crude fibre, per cent	Ether extract, per cent	Ash, per cent	Starch equivalent	Available crude protein, per cent	Starch equivalent	Available energy, kcal/lb
<i>Roots and tubers</i>									
Carrots	13	12	14	0.2	0.9	8.8	0.8	68	1310
Mangolds	12	10	0.7	0.1	0.8	6.2	0.7	52	1290
Potatoes	24	21	0.9	0.1	1.0	18.5	1.1	77	1270
Sugar beet	23	11	1.1	0.1	0.7	11.7	0.8	65	1430
Sugar beet pulp, wet	15	16	3.1	0.1	0.6	6.0	1.0	78	1330
Sugar beet pulp, dried	90	8.9	18.3	0.6	3.1	52	5.3	67	1360
Sugar beet molasses	75	3.5	—	—	5.2	7.3	1.2	69	1300
Swedes	12	13	1.2	0.2	0.7	4.4	1.1	61	1250
Turnips	9	10	0.9	0.2	0.7	—	0.6	49	1110
<i>Cereals and by-products</i>									
Barley	85	9.0	4.5	1.5	2.6	7.1	6.8	84	1400
Barley, brewers' grains, wet	32	7.5	6.1	2.8	1.4	18	5.5	58	1130
Barley, brewers' grains, dried	90	18.3	15.2	6.4	3.9	48	13.0	54	1090
Barley, malt culms	90	24.4	14.0	2.0	7.2	43	19.9	48	1200
Brewers' yeast, dried	94	41.5	0.2	1.0	9.6	68	35.6	73	1210
Maize	87	9.9	2.2	4.4	1.3	7.8	7.9	89	1460
Maize, flaked	89	9.8	1.5	4.3	0.9	8.4	9.4	94	1540
Maize gluten feed	90	23.5	3.5	3.4	2.5	76	20.0	84	1400
Millet	87	10.5	8.1	3.9	3.8	59	8.0	67	1170
Oats	87	10.4	10.3	4.8	3.1	60	8.0	69	1200
Oat husks	94	2.0	33.0	1.0	4.0	21	—	22	540
Oat feed	92	6.0	26.6	1.9	—	26	3.5	28	—
Rice, polished	87	6.7	1.5	0.4	0.8	82	5.8	94	1530
Rye	89	9.6	1.9	3.8	2.4	74	9.6	83	1440
Sorghum	87	12.2	1.9	1.9	1.7	72	10.3	83	1440
Wheat	87	17.0	2.3	4.2	2.4	69	12.6	79	1340
Wheat, fine middlings	86	15.9	6.0	4.5	3.7	57	11.6	66	1340
Wheat, coarse middlings	87	15.1	9.5	3.8	5.8	43	10.9	49	1050

TABLE 2 NUTRITIVE VALUE OF FOODS FOR PIGS

Food	Fresh basis					
	Dry matter, percent	Crude protein, percent	Crude fibre, percent	Ether extract, percent	Ash, percent	Digestible crude protein, percent
Digestible						
Total nutrients, per cent						
Digestible energy, kcal/lb						
<i>Green crops</i>						
Pasture grass closely grazed	20	5.2	3.4	0.8	1.7	3.5
Pasture grass rotational grazing	20	3.4	3.9	0.6	1.6	1.9
Kale, marrow stem, mince	14	2.2	2.5	0.5	1.9	1.4
<i>Roots and tubers</i>						
Carrots	12	1.5	1.1	0.1	1.2	1.0
Mangolds	12	1.5	0.8	0.1	0.9	1.2
Potatoes cooked	24	1.9	0.8	0.1	1.6	1.2
Potato flakes	87	5.5	1.0	0.1	4.0	4.7
<i>Cereals and by-products</i>						
Barley meal	86	10.5	4.8	1.5	2.6	8.6
Brewers' yeast, dried	94	41.5	0.2	1.0	9.6	37.1
Maize meal	87	9.6	2.0	4.4	1.6	7.5
Maize, flaked	89	10.4	1.5	4.4	1.1	9.9
Oats, fine ground	87	11.6	11.4	5.6	3.6	8.7
Oats, crushed	87	9.7	11.1	4.8	3.2	6.7
Sorghum	90	11.9	2.1	2.9	1.8	8.5
Wheat	87	13.2	2.7	1.8	1.9	10.6
Fine middlings * (85 per cent extr.)	87	14.1	10.3	4.3	4.9	9.0
Coarse middlings (85 per cent. extr.)	87	12.3	13.4	3.9	6.0	6.7

TABLE 3 NUTRITIVE VALUE OF FOODS FOR POULTRY

Food	Fresh basis						Metabolisable energy, kcal/lb
	Dry matter, per cent	Crude protein, per cent	Ether extract, per cent	Ash, per cent	Digestible crude protein, per cent	Digestible ether extract, per cent	
<i>Green crops and tubers</i>							
Dried grass	87	14.8	5.3	7.5	13.0	4.1	610
Dried lucerne	89	14.5	2.7	7.3	12.3	1.1	500
Potato meal	91	8.7	0.2	3.2	6.3	—	1340
<i>Cereals and by products</i>							
Barley	86	11.0	2.1	2.4	8.8	1.6	1240
Brewers yeast, dried	87	42.5	2.1	8.9	37.4	1.6	1190
Maize	85	9.8	3.6	1.1	8.4	3.2	1510
Maize gluten feed	90	25.0	1.9	5.3	22.3	1.1	1060
Millet	86	11.9	3.9	2.9	8.2	2.8	1300
Oats	85	9.0	4.3	3.5	7.4	4.0	1080
Sorghum (milo)	86	9.7	2.8	1.4	8.4	2.5	1410
Wheat	84	9.8	1.7	1.4	7.9	0.9	1380
Wheat germ meal	89	24.8	7.3	4.3	19.8	6.2	1210
Wheat, coarse middlings	87	15.9	5.1	4.3	12.7	4.1	1060
Wheat, fine middlings	87	17.7	5.2	3.2	15.0	4.5	1280

TABLE 3 concluded

<i>Oilseed by-products</i>								
Coconut meal	89	19.5	6.7	6.4	10.9	6.2	15.6	750
Cottonseed meal (dec , exp)	90	37.8	6.1	6.7	28.0	5.4	23.6	1180
Groundnut meal (dec , extr)	87	42.7	1.5	5.2	37.8	1.4	26.2	1240
Groundnut meal (dec , exp)	92	49.5	5.3	5.8	43.6	4.7	22.6	1430
Linseed meal (exp)	89	34.1	6.3	5.3	30.0	5.5	8.2	940
Palm kernel meal (extr)	90	19.0	2.0	4.0	17.1	1.9	18.2	730
Palm kernel meal (exp)	90	16.6	10.2	4.0	14.9	9.7	16.7	990
Soya bean meal (extr)	87	42.4	1.7	6.8	37.9	1.3	24.9	1220
Sunflower seed meal (dec)	89	35.6	2.8	6.4	29.9	2.6	10.1	860
<i>Leguminous seeds</i>								
Bean meal	85	25.3	0.9	2.8	10.6	0.6	32.5	830
Pea meal	87	27.1	1.7	2.8	20.6	1.4	41.1	1200
<i>Animal by-products</i>								
Blood meal	87	80.0	0.8	3.5	72.0	0.7	2.5	1410
Fish meal, white	92	63.2	4.4	21.3	55.0	3.8	1.6	1290
Meat meal	90	72.2	13.2	3.8	65.0	11.9	—	1700
Meat and bone meal	92	50.0	9.5	29.0	45.0	8.6	—	1190
Milk, dried skim	93	34.0	0.9	8.0	27.5	0.8	42.9	1330
Milk, dried whey	94	12.5	0.7	8.5	10.1	0.6	58.3	1300
Whale meal	92	60.0	16.0	16.0	—	—	—	1550
Whale solubles	58	47.7	0.9	5.6	—	—	—	800

TABLE 4 AMINO ACID COMPOSITION OF FOODS (PER CENT. OF FOOD)

Food	Crude protein	Arginine	Cystine	Glycine	Histidine	Leucine	Isoleucine	Lysine	Methionine	Phenylalanine	Threonine	Tryptophan	Tyrosine	Valine
<i>Green crops and tubers</i>														
Dried grass	14.8	0.99	0.19	0.72	0.46	1.98	1.38	1.06	0.31	1.30	0.89	0.31	0.46	1.57
Dried lucerne	14.5	0.51	0.25	0.52	0.22	0.62	1.15	0.61	0.19	0.59	0.73	0.22	0.26	0.71
Potato meal	8.2	0.43	—	—	0.11	0.48	0.30	0.47	0.07	0.29	0.21	0.15	—	0.39
<i>Cereals and by products</i>														
Barley	12.7	0.55	0.23	0.35	0.24	0.67	0.50	0.40	0.17	0.56	0.37	0.15	0.22	0.56
Brewers' yeast, dried	42.5	2.12	0.89	2.55	1.74	3.18	1.91	2.84	0.59	0.80	3.48	0.38	1.74	3.99
Maize	9.8	0.57	0.19	0.31	0.22	1.10	0.38	0.27	0.20	0.45	0.48	0.11	0.39	0.73
Maize gluten feed	25.0	1.10	—	—	0.78	2.64	0.92	0.84	0.54	0.98	0.92	0.18	0.35	1.42
Millet	11.9	0.35	0.08	—	0.23	1.23	0.49	0.25	0.30	0.59	0.44	0.17	—	0.62
Oats	9.0	0.60	0.16	0.37	0.14	0.51	0.46	0.31	0.14	0.43	0.31	0.12	0.29	0.59
Sorghum (milo)	11.3	0.45	—	—	0.24	1.37	0.54	0.28	0.11	0.49	0.32	0.11	0.19	0.57
Wheat	9.8	0.47	0.30	—	0.22	0.68	0.37	0.27	0.14	0.49	0.36	0.15	0.09	0.44
Wheat germ meal	24.8	1.83	0.35	—	0.57	1.47	0.86	1.63	0.41	0.98	0.98	0.26	0.73	1.24
Wheat, fine middlings	17.7	1.13	0.33	—	0.50	1.08	0.66	0.71	0.32	0.68	0.62	0.28	0.50	0.91
Wheat, coarse middlings	15.9	0.96	0.30	—	0.36	0.93	0.58	0.66	0.24	0.57	0.49	0.30	0.21	0.78

TABLE 4 *continued*

<i>Oilseed by-products</i>														
Coconut meal	20.0	2.20	—	—	0.31	1.21	1.06	0.52	0.25	0.78	0.62	0.15	0.80	1.03
Cottonseed meal (dec., exp.)	37.8	4.18	0.83	—	1.02	2.35	1.52	1.60	0.56	2.00	1.32	0.60	1.21	1.89
Groundnut meal (dec., extr.)	52.3	5.84	—	—	1.14	3.65	1.98	2.28	0.36	2.63	1.46	0.49	1.93	2.82
Groundnut meal (dec., exp.)	49.5	5.15	—	—	1.10	3.35	2.15	1.75	0.50	2.50	1.50	0.60	1.81	2.40
Linseed meal (exp.)	34.1	3.17	0.31	0.23	0.61	2.04	1.56	1.23	0.57	1.54	1.29	0.60	0.75	1.90
Palm kernel meal (extr.)	19.0	2.54	—	—	0.31	1.23	0.76	0.66	0.41	0.82	0.60	0.20	0.63	1.03
Palm kernel meal (exp.)	16.6	2.22	—	—	0.27	1.07	0.66	0.58	0.36	0.72	0.52	0.17	0.55	0.90
Soya bean meal (extr.)	56.9	3.01	—	—	1.70	4.49	3.52	3.01	0.91	2.78	3.10	0.62	1.19	3.01
Soya bean meal (exp.)	47.5	2.80	—	—	1.19	3.99	2.90	3.18	0.38	2.19	2.19	0.52	1.09	3.16
Sunflower meal (dec.)	35.6	3.00	0.55	—	0.62	2.27	1.91	1.39	1.25	2.09	1.46	0.48	0.95	1.91
<i>Leguminous seeds</i>														
Bean meal	25.3	1.74	0.28	0.92	0.72	1.25	1.28	1.80	0.29	1.35	1.22	0.36	0.78	1.38
Pea meal	27.1	2.06	0.19	—	0.65	1.86	1.81	2.09	0.49	1.17	1.06	0.22	0.98	1.14
<i>Animal by-products</i>														
Blood meal	80.0	3.37	—	—	4.25	11.1	0.99	3.87	1.28	5.80	4.34	1.17	2.21	7.76
Fish meal	60.0	3.91	0.60	—	1.11	4.00	2.48	4.07	1.56	2.02	2.46	0.61	1.95	2.70
Herring meal	63.7	3.64	—	—	1.51	5.19	3.66	5.22	1.86	2.58	2.88	0.99	2.20	3.86
Meat meal	72.2	3.91	—	—	2.54	5.80	2.46	4.41	0.80	3.69	2.54	0.43	1.59	4.41
Meat and bone meal	50.0	3.74	—	—	0.90	3.22	1.74	2.81	0.68	1.75	1.70	0.35	1.22	2.45
Milk, fresh	3.6	0.14	—	—	0.11	0.36	0.25	0.24	0.06	0.16	0.16	0.06	—	0.27
Milk, dried skim	34.0	1.00	0.23	6.07	1.07	3.07	2.40	2.40	0.73	1.67	1.40	0.34	0.73	2.00
Milk, dried whey	12.5	0.16	0.32	—	0.16	0.96	3.17	0.80	0.72	0.08	0.38	0.59	0.08	0.56
Whale meal	60.0	2.50	0.74	—	1.19	4.29	2.73	8.00	3.00	2.07	1.64	0.83	—	2.82
Whale solubles	47.7	2.50	0.24	6.00	1.00	2.40	1.10	3.00	0.44	1.20	1.60	0.30	0.80	2.10

Food	Carotene ppm	Vitamin E ppm	Thiamine ppm	Riboflavin ppm	Nicotinic acid ppm	Pantothenic ac ppm	Vitamin B ₆ ppm	Vitamin B ₁₂ ppm	Choline ppm
<i>Cereals and by-products</i>									
Barley	0.4	6.2	5.2 91.7	2.0 35.0	6.0 4.8	6.6 11.0	3.0	—	1050 3890
Brewers' yeast, dried	—	—	4.2	1.4	22	5.6	7.6	—	570
Malt	4.0	—	6.4	1.6	16	13.2	1.2	—	1100
Oats	—	6.0	2.8	0.6	36	6.4	6.4	—	920
Rice	—	7.2	4.0	1.6	13	7.0	5.4	—	—
Rye	1.2	15.8	4.2	1.4	44	11.4	4.8	—	700
Sorghum	—	—	5.0	1.2	58	12.2	—	—	850
Wheat	—	—	—	2.4	95	—	—	—	1168
Wheat, fine middlings	—	20.0	—	2.2	100	—	—	—	1109
Wheat, coarse middlings	—	—	0.7	3.1	25	6.6	—	—	920
<i>Oilseed by-products</i>									
Coconut meal	—	—	—	4.8	33	—	—	—	2607
Cottonseed meal (dec., exp.)	—	18.9	7.3	11.0	170	53	—	—	2000
Groundnut meal (dec., exp.)	—	—	7.3	5.3	169	48	—	—	1683
Groundnut meal (dec., exp.)	0.2	—	9.5	2.9	30	—	—	—	1225
Linseed meal (extr.)	—	—	—	—	—	—	—	—	—
Palm kernel meal (extr.)	0.2	1.1	6.6	3.3	27	15	—	—	2743
Soya bean meal (extr.)	—	—	—	—	—	—	—	—	3100
<i>Animal by-products</i>									
Fish meal, white	—	21.0	—	6.6	62	—	—	0.10	4004
Herring meal	—	—	—	9.0	89	11.4	5.7	0.22	2427
Meat meal	—	—	—	5.5	55	—	—	0.04	2207
Meat and bone meal	—	—	—	5.3	51	—	—	—	130
Milk, cow's, whole	—	—	—	1.6	0.9	3.5	0.5	0.01	1078
Milk, dried skim	0.4	0.6	0.4	2.09	12	—	—	0.06	1549
Milk, dried whey	—	0.4	—	26.6	11	—	—	0.02	3395
Whale meal	—	—	—	4.0	125	—	—	0.05	1998
Whale solubles	—	—	—	2.0	97	—	—	0.02	—

TABLE 6 MINERAL CONTENT OF FOODS

Food	Dry matter per cent	Ash per cent	Calcium per cent	Phosphorus per cent	Magnesium per cent	Sodium per cent	Iron ppm	Manganese ppm	Copper ppm	Cobalt ppm	Zinc ppm
Grass and forage crops (Dry matter basis)											
Perennial ryegrass, young leafy	100	—	0.66	0.30	0.31	0.19	333	31	15.2	—	—
Perennial ryegrass, mature	100	—	0.45	0.25	0.24	0.10	181	18	6.5	0.14	—
Cocksfoot, young leafy	100	—	0.64	0.31	0.25	0.15	321	61	7.0	0.20	—
Cocksfoot, mature	100	—	0.34	0.25	0.21	0.11	167	36	15.0	0.21	—
Chicory	100	—	1.40	0.48	0.64	0.27	469	58	12.5	0.20	—
Plantain	100	—	1.62	0.33	0.60	0.30	490	35	10.5	0.20	—
Lucerne	100	—	2.10	0.40	0.54	0.07	291	37	9.1	0.15	—
Red clover	100	8.7	1.76	0.29	0.45	0.26	299	158	8.8	0.13	—
Silages											
Ryegrass	24	3.2	0.16	0.08	0.08	—	—	—	1.1	—	—
Lucerne	30	2.8	0.48	0.11	0.10	0.05	86	15	2.9	0.05	—
Red clover	28	2.6	0.43	0.06	0.11	0.06	—	—	—	—	—
Hays											
Ryegrass	88	7.4	0.43	0.28	0.30	—	815	53	4.6	0.11	—
Timothy	88	4.9	0.33	0.17	0.15	0.11	110	57	4.4	0.08	15
Lucerne	88	8.0	1.43	0.23	0.28	0.14	209	46	12	0.11	15
Straws											
Barley	88	5.8	0.30	0.08	0.17	0.11	283	15	—	—	—
Oat	90	7.4	0.30	0.09	—	—	170	36	9.2	—	—
Rye	89	4.3	0.25	0.09	0.07	0.12	—	6	3.6	—	—
Wheat	90	7.3	0.15	0.07	0.11	0.14	134	36	3.0	0.04	—
Continued overleaf											

Continued overleaf

ANIMAL NUTRITION

TABLE 6 continued

	Dry matter per cent	Ash per cent	Calcium per cent	Phosphorus per cent	Magnesium per cent	Sodium per cent	Iron ppm	Manganese ppm	Copper ppm	Cobalt ppm	Zinc ppm
<i>Food</i>											
<i>Roots and tubers</i>											
Carrots	10	—	0.05	0.02	0.01	0.10	56	—	0.8	—	—
Potatoes	25	—	0.02	0.04	0.03	0.01	26	7	—	—	—
Sweedes	86	—	0.06	0.02	0.01	0.05	35	—	0.5	—	—
Turnips	67	—	0.06	0.03	0.01	0.06	37	—	0.7	—	—
<i>Cereals and by-products</i>											
Barley	89	2.7	0.08	0.42	0.13	0.02	54	16	7.8	0.10	16
Brewers' yeast, dried	93	6.4	0.13	1.43	0.23	0.07	128	57	33	0.18	39
Maize	86	1.1	0.03	0.27	0.12	—	17	51	2.1	—	17
Millet	90	3.2	0.05	0.28	0.16	0.04	44	29	22	0.04	14
Oats	89	3.2	0.10	0.35	0.17	0.06	72	39	6	0.06	—
Rice	89	1.4	0.04	0.23	0.06	0.04	36	18	3.3	—	1.8
Rye	89	1.7	0.06	0.34	0.12	0.02	80	68	7.8	—	31
Sorghum	89	1.7	0.04	0.29	0.20	0.01	20	13	14.1	0.10	14
Wheat, fine middlings	87	1.6	0.05	0.36	0.16	0.09	54	50	7.2	0.08	14
Wheat, coarse middlings	87	3.2	0.05	0.70	—	—	—	95	—	—	68
Wheat, bran	86	4.3	0.07	0.90	—	—	—	84	—	—	106
		4.9	0.14	1.30	—	—	—	122	—	—	162

TABLE 7 FEEDING STANDARDS FOR DAIRY CATTLE

1 *Maintenance* (Daily requirements)

<i>Liveweight lb</i>	<i>Starch equivalent lb</i>	<i>Digestible crude protein lb</i>	<i>Calcium g</i>	<i>Phosphorus g</i>
800	5.1	0.51	13	19
900	5.5	0.55	15	22
1000	6.0	0.60	16	23
1100	6.5	0.65	18	26
1200	6.9	0.69	19	28

2 *Lactation* (Requirements per lb milk)

<i>Fat content of milk per cent</i>	<i>Starch equivalent lb</i>	<i>Digestible crude protein lb</i>	<i>Calcium g</i>	<i>Phosphorus g</i>
3.5	0.27	0.051	1.2	0.8
4.0	0.29	0.056	1.3	0.8
4.5	0.31	0.063	1.3	0.8
5.0	0.33	0.070	1.4	0.8

3 *Pregnancy* (Daily requirements add to maintenance during last 2 months)

<i>Starch equivalent lb</i>	<i>Digestible crude protein lb</i>	<i>Calcium g</i>	<i>Phosphorus g</i>
5	0.6	17	9

TABLE 8 FEEDING STANDARDS FOR BEEF CATTLE

Live weight (lb)	Starch equivalent (lb) for growth (per lb live weight gain)		Digestible crude protein (lb/day) for maintenance and growth		Minerals (g/day) for maintenance and growth					
					Calcium			Phosphorus		
	Slow growth (c. 1 lb/day)	Fast growth (c. 2 lb/day)	Slow growth (c. 1 lb/day)	Fast growth (c. 2 lb/day)	Slow growth (c. 1 lb/day)	Fast growth (c. 2 lb/day)	Slow growth (c. 1 lb/day)	Fast growth (c. 2 lb/day)	Slow growth (c. 1 lb/day)	Fast growth (c. 2 lb/day)
400	1.55	—	0.75	—	19	32	9	14		
600	1.85	2.1	0.85	1.10	21	33	13	18		
800	2.15	2.4	0.90	1.20	24	35	20	25		
1000	2.45	2.6	0.95	1.25	27	38	27	31		

TABLE 9 FEEDING STANDARDS FOR SHEEP

1 Maintenance (Daily requirements)

Liveweight	Starch equivalent	*Digestible crude protein	Calcium	Phosphorus
lb	lb	lb	g	g
60	0.73	0.09	2.0	1.5
80	0.90	0.11	2.9	2.0
100	1.07	0.13	4.0	2.8
120	1.23	0.15	4.9	3.7
140	1.38	0.17	5.7	4.6
160	1.52	0.19	6.5	5.3

* These values include a requirement for wool production, but will be slightly lower for the hill breeds

2 Growth and fattening (Requirements per lb liveweight gain)

Liveweight	Starch equivalent	Digestible crude protein	Calcium	Phosphorus
lb	lb	lb	g	g
60	1.5	0.23	7.3	2.8
80	1.8		8.1	2.8
100	2.0		9.0	3.2
120	2.5		9.0	3.5
140	3.0		9.0	3.8
160	3.8		9.0	3.8

3 Pregnancy (Daily requirements of ewe, last 6 weeks)

Liveweight	Starch equivalent	Digestible crude protein	Calcium	Phosphorus
lb	lb	lb	g	g
120	1.83	0.26	8.1	5.4
140	1.98	0.28	8.9	6.3
160	2.12	0.30	9.6	7.0

4 Lactation (Total daily requirements)†

Liveweight	Starch equivalent	Digestible crude protein	Calcium	Phosphorus
lb	lb	lb	g	g
(i) First 10 weeks				
100	2.97	0.54	13.0	8.3
120	3.13	0.56	13.9	9.2
140	3.28	0.58	14.7	10.1
160	3.42	0.60	15.5	10.8
(ii) Latter part of lactation				
100	2.02	0.34	8.5	5.6
120	2.18	0.36	9.4	6.5
140	2.33	0.38	10.2	7.4
160	2.47	0.40	11.0	8.1

† Assuming a milk yield of $4\frac{1}{2}$ lb/day in first 10 weeks and half this quantity in the latter part of lactation

TABLE 10 FEEDING STANDARDS FOR PIGS

Liveweight (lb)	Young pigs			Baconers			Preg- nant sows	Lac- tating sows
	3-10	10-20	20-50	50-100	100-150	150-200		
DE (kcal/lb)	2175	1625	1525	1500	1400	1400	1500	1500
Crude protein (per cent)	30*	23†	17‡	16§	15§	14§	14	17
<i>Amino acids (per cent)</i>								
Histidine	0.45	0.30	0.20	—	—	—	—	—
Isoleucine	1.15	0.75	0.50	—	—	—	—	—
Leucine	1.44	0.97	0.64	—	—	—	—	—
Lysine	1.44	0.97	0.75	—	—	—	—	—
Methionine	1.20	0.79	0.52	—	—	—	—	—
+cystine								
Phenylalanine	1.05	0.72	0.47	—	—	—	—	—
+tyrosine								
Threonine	0.91	0.61	0.40	—	—	—	—	—
Tryptophan	0.31	0.20	0.13	—	—	—	—	—
Valine	1.01	0.64	0.44	—	—	—	—	—
<i>Vitamins</i>								
A (I U/lb)	1000	1000	800	600	600	600	1500	1500
D (I U/lb)	100	90	90	90-60	60	60	60	60
Thiamine (ppm)	1.7	1.3	1.2	1.1	1.1	1.1	1.1	1.1
Riboflavin (ppm)	3.3	3.1	2.6	2.2	2.2	2.2	3.3	3.3
Nicotinic acid (ppm)	22	16	15	15-11	11	11	18	18
Pantothenic acid (ppm)	13	11	11	10	10	10	13	13
Vitamin B ₆ (ppm)	1.1	1.1	1.1	—	—	—	—	—
Vitamin B ₁₂ (ppm)	0.022	0.022	0.015	0.011	0.011	0.011	0.011	0.011
<i>Minerals</i>								
Calcium (per cent)	1.05	1.00	0.7-0.5	0.5	0.5	0.5	0.6	0.6
Phosphorus (per cent)	0.85	0.80	0.6-0.4	0.4	0.4	0.4	0.4	0.4
Chlorine (per cent.)	0.09	0.09	0.16	—	—	—	—	—
Copper (ppm)‡	22	20	20	—	—	—	—	—
Iron (ppm)	110	100	100	—	—	—	—	—
Magnesium (ppm)	—	462	440	—	—	—	—	—
Manganese (ppm)	—	40	37	—	—	—	—	—
Potassium (per cent)	0.43	0.45	0.30	—	—	—	—	—
Sodium (per cent)	0.14	0.14	0.10	—	—	—	—	—
Zinc (ppm)‡	—	100	100	—	—	—	—	—

Notes —

* All protein from dried milk.

† Mixed proteins from cereals, dried milk and high protein foods.

‡ Mixed proteins from cereals and high-protein foods such as fish meal and soya bean meal.

§ May be higher with poor-quality protein.

|| Levels which have prevented signs of deficiency, but are probably above minimum requirements.

TABLE 11 FEEDING STANDARDS FOR POULTRY

TABLE 11. FEEDING STANDARDS		Liveweight (lb)			
1 Energy * (kcal ME per day)		<div>3456</div>			
	Egg production	3	4	5	6
Maintenance		165	230	285	335
Maintenance and production	20 per cent	190	255	310	360
	40 per cent	220	280	335	385
	60 per cent	245	305	360	410
	80 per cent	270	330	385	435

2. Amino acids † (per cent of air dry diet)			
	Chicks (0-4 weeks)	Layers	Turkey poult (0-6 weeks)
Arginine	0.8	—	—
Glycine	1.0	—	0.9
Histidine	0.35	—	—
Isoleucine	0.5	0.5	0.8
Leucine	1.5	0.7	—
Lysine	1.0	0.5	1.5
Methionine + cystine	0.7	0.55	0.9
Phenylalanine + tyrosine	1.2	0.7	—
Threonine	0.55	0.4	—
Tryptophan	0.15	0.13	0.25
Valine	0.8	0.55	—

3 Vitamins ‡ (concentration in air-dry diet)				
	Chicks (first few weeks)	Layers	Breeders	Turkey poult
A (I U /lb)	700	2000	3000	800
D ₃ (I U /lb)	1.40	270	270	500
B ₆ (menaphthone) (ppm)	0.29	—	—	—
Thiamine (ppm)	1.0	—	—	1.0
Riboflavin (ppm)	4.0	2.5	4.0	3.5
Nicotinic acid (ppm)	28	—	—	20-50
Pantothenic acid (ppm)	10	1.5	6.5	10.5
Vitamin B ₁₂ (ppm)	3.5	2.0	4.0	3.0
Biotin (ppm)	0.03-0.05	—	0.15	—
Folic acid (ppm)	1.5	0.30	0.5	1.5
Vitamin B ₁₂ (ppm)	0.02	—	0.002	0.004
Choline (ppm)	1300	—	1100	1400

TABLE 11 *concluded*

. Minerals § (concentration in air-dry diet)

	<i>Chicks (first few weeks)</i>	<i>Turkey poult</i> s
Calcium (per cent)	1.0	1.5
Phosphorus (per cent)	0.43	0.6
Chlorine (per cent)	0.06	—
Copper (ppm)	3.2	—
Iodine (ppm)	0.35	—
Iron (ppm)	40	—
Magnesium (ppm)	250	—
Manganese (ppm)	35	—
Potassium (per cent)	0.2	—
Sodium (per cent)	0.11	—
Zinc (ppm)	15	—

Notes —

The requirements for some nutrients are influenced by the energy level of the diet. The figures given in the above table, except when otherwise stated, relate to diets of energy content around 2.8 Mcal ME/kg (1270 kcal ME/lb). For fuller details about individual nutrients, the reader is referred to the A.R.C. publication on the nutrient requirements of poultry (Reference No. 1).

* The energy requirements vary depending upon the microclimate surrounding the laying hen, and will be about 5 per cent. higher in winter and 5 per cent. lower in summer than the values given.

$$\text{Per cent. production} = \frac{\text{No. of eggs laid}}{\text{No. of days in observation period}} \times 100.$$

† Methionine can be replaced in part by cystine, although about 40 per cent. of the combined requirement should be in the form of methionine. Similarly phenylalanine can be replaced in part by tyrosine, but at least 50 per cent. of the combined requirement should be in the form of phenylalanine.

The figures in *italics* relate to purified diets containing about 3.1 Mcal ME/kg (1410 kcal ME/lb).

‡ The requirements for vitamin E are ill defined and it is not possible to give reliable estimates.

§ The calcium requirement of the laying hen varies with the level of production, ranging from 2g/day at 40 per cent. production to 4g/day at 80 per cent. production.

The phosphorus value is that quantity of inorganic phosphorus which, when supplemented by the phosphorus contributed by the plant materials in the diet, will satisfy the requirements. The requirement of the laying hen is about 0.3 g/day.

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INDEX

- Abomasum, 107, 114, 116, 119
- Abortion, 52, 92
- Absorption, 55, 104, 112-114, 116ff
- Acetic acid, in large intestine, 110
 - in rumen, 115, 117, 188
 - in silage, 307, 309
 - metabolism of, 125ff
 - utilisation of, for fattening, 176, 178
 - for maintenance, 173
 - for milk production, 179, 268ff, 275, 276, 285
- Acetoacetate, 266
- Acetone, 12, 266
- Acetyl choline, 70
- Acetyl coenzyme A, 98, 125ff, 266
- Achillea millefolium* (see yarrow)
- Acidosis, 266
- Ackerman factor, 355
- Actin, 125
- Activators, 100
- Activity increment, 221
- Acyl coenzyme A, 132, 141
- Adenine, 42-44, 124, 138, 309
- Adenosine, 42, 43, 124
- Adenosine diphosphate (ADP), 124ff
- Adenosine monophosphate (AMP), 43, 124ff
- Adenosine triphosphate (ATP), 124ff, 162, 172, 173, 177
- Adenylic acid (see adenosine monophosphate)
- Aflatoxin, 347
- Agar, 19
- Agrostis* spp. (see bents)
- A.I.V. silage, 307
- Alanine, 36, 44, 66, 135, 138
- Albumins, 40, 41, 267, 268
- Aldehydes, 28
- Aldoses, 8, 15
- Alimentary canal, 106ff
- Alkali disease, 94
- Alkaloids, 44, 46, 47, 201
- Allantoin, 159
- Aluminium, 269
- Amides, 44, 46, 201, 296, 301
- Amines, 44, 45, 309
- Amino acids, 34ff
 - Amino acids, absorption of, 113, 120
 - as products of digestion, 110, 119, 211
 - as source of energy, 133, 275
 - available, 209
 - chemical properties of, 34
 - deamination of, 118-120, 133
 - essential (see Essential amino acids)
 - formulae of, 36
 - in cereals, 331ff
 - in grass, 296
 - in milk, 267, 268
 - in protein concentrates, 345ff
 - in protein synthesis, 135ff, 162, 200, 201, 206, 207
 - in silage, 309
 - katabolism of, 133
 - requirements of pigs, 242ff, 293
 - poultry, 242ff, 260
 - ruminants, 226
 - synthesis of, 135, 175
- Aminopeptidases, 105, 106, 109
- Ammonia, in metabolism, 133, 134
 - in milk, 268
 - in rumen, 84, 118-120, 211, 212
 - in silage, 309
- Ammonium salts, 201
- Amygdalin, 12
- Amylase, 104, 105, 108-112
- Amylopectin, 16, 17, 332
- Amylose, 16, 332
- Anabolism, 123
- Anaemia, copper deficiency, 86
 - iron deficiency, 85, 113, 264, 265
 - pernicious, 70
- Androgens, 363
- Animal protein concentrates, 351ff
- Animal Protein Factor (APF), 70, 352, 353
- Anomers, 9
- Antibiotics, 358ff
- Antioxidants, 28, 29, 58
- Anti pernicious anaemia factor (APA), 70
- Apo-enzyme, 100
- Arabans, 7, 15
- Arabinose, 10, 11, 15, 18, 19
- Arachidic acid, 22, 30

- Arachidonic acid, 22, 23
 Arginase, 100
 Arginine, 45, 106, 134, 243-245, 293, 296
 as essential amino acid, 38, 207
 formula, 37
 in protein synthesis, 136
 Armsby, H. P., 183, 184, 188
 Arsenic acid, 366
 Arsenic, 94, 102, 269
 Arsenicals, 366
 Arsonic acid, 366
 Ascorbic acid (see Vitamin C)
 Ash, 3, 4, 158, 235, 258, 272
 Asparagine, 46, 296
 Asparagosan, 18
 Aspartic acid, 36, 44, 46, 133
 in protein synthesis, 135
 Aspartic deaminase, 133
Aspergillus flavus, 347
 Associative effect of foods, 150, 179, 193
Astragulus bisulcatus, 94
 Atherosclerosis, 32
 Atropine, 47
Avena sativa (see oats)
 Avidin, 69
 Autocatalysis, 108

 Bacitracin, 358, 360, 361
 Bacteria, in digestive tract, 110ff
 in silage, 306ff
 Barium, 76, 95
 Barley, by products, 334ff
 feed, 336
 grain, 14, 331, 334ff
 straw, 323
 Basal metabolism, 157, 165, 177, 217,
 218, 227, 263, 291
 Beans, 61, 303
 Beeswax, 30
 Bents, 298
 Beri beri, 48
Beta vulgaris, 324
 Betaine, 45, 46, 309, 328
 Bile, 108, 109, 112, 114
 Bilirubin, 109
 Biliverdin, 109
 Biological oxidation, 124
 Biological value, (BV), 204ff, 240, 242,
 278, 294
 for wool growth, 246
 in factorial calculations, 228
 of food proteins, 206, 345
 of microbial protein, 212
 Biotin, 69, 82, 139, 270, 282

 Black tongue, 64
 Blaxter, K. L., 195, 197, 225, 276
 Blind staggers, 94
 Bloat, 118, 303, 334
 Blood, 3
 dried, 355
 minerals in, 76ff
 Bloodmeal, 86, 355
 Bomb, calorimeter, 157, 171, 274
 Bone, 55, 77, 95
 Bone flour, 78
 Boron, 269
 Bracken poisoning, 62
 Bran, 328, 337-339
Brassica napobrassica (see swedes)
Brassica rapa (see turnips)
 Brassicas, 303, 326
 Brewers' grains, 328, 335
 Brewers' yeast, 335, 336
 Bromine, 76, 95, 269
 Brunner's glands, 109
 Bumet, 299
 Butter, 26, 348
 Butterfat, 26, 27, 158, 179, 267ff
 Butylated hydroxyanisole, 29
 Butyric acid, 22, 26, 27, 110
 in rumen, 117
 in silage, 309
 utilisation of, 173, 176
 Butyryl coenzyme A, 140

 Cabbages, 303, 304
 Cadaverine, 45
 Caeca, 111, 112
 Caecum, 107, 110, 121
 Calciferols, 54
 Calcium, 76ff, 149
 absorption of, 113
 availability of, 152, 153
 deficiency symptoms, 77, 78, 265
 in animal body, 76, 77, 248
 in eggs, 258
 in milk, 267, 269, 279, 287, 289
 interrelations with, magnesium, 83
 manganese, 92
 phosphorus, 78
 Vitamin D, 55, 77
 zinc, 93, 114
 requirements for, egg production, 259
 lactation, 280, 281, 287, 289, 294
 maintenance and growth, 248, 249
 reproduction, 257
 sources of, 78
 Calcium phosphate, 78

- Calorie, 123
 Calorific values, 158, 170
 Calorimeter, animal, 163-165, 183
 bomb, 157, 171, 274
 gradient layer, 164, 165
 Calorimetry, direct, 163-165
 indirect, 163, 165ff
 Calves, feeding of antibiotics to, 361
 mineral deficiencies in, 77ff
 rumen flora in, 116
 vitamin deficiencies in, 52ff, 250
 Cannibalism, 82, 259
 Caponisation, 363, 365
 Capric acid, 22, 26
 Caproic acid, 22, 26, 28
 metabolism of, 132, 135
 Capryl coenzyme A, 140
 Caprylic acid, 22, 26
 Carbamic acid, 133, 134
 Carbamyl phosphate, 134
 Carbohydrases, 104
 Carbohydrates, 2, 6ff
 absorption of, 112
 classification of, 6, 7
 determination of, 5
 digestion of, 104ff, 116ff, 148
 in eggs, 258
 in grasses, 295, 298, 302
 in milk, 268
 in silage, 308-312
 metabolism of, 126ff
 oxidation of, 126ff, 166
 utilisation of, for maintenance, 173
 for production, 176ff
 Carbon balance, 163, 169-171
 Carbon dioxide, in rumen, 117, 118
 in respiration, 126ff, 168
 Carbonic anhydrase, 92
 Carboxypeptidase, 92, 105, 106, 109
 Carmine, 145
 Carnaubic acid, 29
 Carnaubyl alcohol, 29
 Carotenes, 49-51, 56, 114, 260
 in grasses, 297, 319, 320
 in hay, 315
 in milk, 282
 in silage, 310
 (see also Vitamin A)
 Carrots, 51, 328
 Casein, 41, 158, 176, 267, 268, 356
 iodinated, 363
 Cassava, 12
 Catalyst, 97
 Cattle, digestibility trials with, 145, 151
 digestion in, 107
 energy utilisation by, 173, 176
 feeding standards for, growth and fattening, 231ff
 lactation, 270ff
 maintenance, 214ff
 reproduction, 253
 liveweight gain, 235, 237
 mineral requirements of, 247-249
 protein requirements of, 211-213, 228-231, 239-241
 vitamin deficiencies in, 52ff
 (see also ruminants)
 Cellobiose, 6, 13, 14, 17
 Cellulases, 17
 Cellulose, 7, 15, 17, 18, 150, 158, 185, 188
 digestion, in fowls, 112
 in horses, 121
 in pigs, 109, 110
 in ruminants, 115-118
 in grass, 295, 299, 300
 Cephalins, 21, 30, 31
 Cereal, forage, 303, 308
 grains, 16, 56, 61, 69, 150, 331ff
 hay, 316
 straws, 151, 321ff
 Cerebrosides, 31
 Cetyl alcohol, 29
 Chaff, 321, 323
 Chaffing of foods, 150, 151
 Cheese, 28
 Chemical score, 208, 209, 345
 Chick (see poultry)
 Chicory, 299
 Chlorine, 76, 81, 258, 259
 in milk, 269
 Chlorophyll, 309
 Chlorpromazine, 367
 Chlorotetracycline, 358-362
 Choline, 31
 Cholecalciferol, 53, 54 (see also Vitamin D)
 Cholesterol, 32, 246, 268
 Choline, 21, 30, 31, 45, 69, 70, 270
 Chopping of foods, 150
 Chrome oxide, 147
 Chromoproteins, 41
 Chymotrypsin, 105-109
 Chymotrypsinogen, 108, 109
Cichorium intybus (see Chicory)
 Citric acid, 98, 128, 159
 Citrulline, 134
 Cloaca, 107, 111, 145
 Clostridia, 306
 Clovers, 118, 298, 299, 305

- Clubbed down, 63
- Cobalamins (see Vitamin B₁₂)
- Cobamide coenzyme, 72
- Cobalt, 72, 76, 88, 89, 121, 297, 298, 300
- Cocaine, 47
- Coccarboxylase, 61
- Cocksfoot, 293, 298
- Coconut meal, 349
 - oil, 26
- Codliver oil, 48, 50, 54, 57, 286
- Coenzyme A, 66, 67, 98, 100, 125ff
- Coenzymes, 10, 100
- Collagen, 137
- Colon, 107, 109, 121
- Colostrum, 54, 270
- Comparative slaughter techniques, 171, 198, 220, 234, 240
- Compositae, 18
- Conine, 47
- Cooking of foods, 150, 151
- Copper, 76, 86ff
 - deficiency symptoms, 86, 93, 265
 - in eggs, 258
 - in milk, 270
 - in pasture, 87, 297, 298
 - in wool production, 247
 - sources of, 87
 - toxicity of, 87, 88, 366
- Copper sulphate, 366
- Cortisol, 266
- Cottonseed, 15
 - cake, 84, 344
 - meal, 348
- Cow (see cattle and ruminants)
- Crazy chick disease, 58
- Creatine, 126, 226, 267, 268
- Creatinine, 159, 226
- Crop (of fowl), 107, 111, 112
- Crude fibre, 4, 5
 - determination of, 5
 - effect on, digestibility, 149, 150
 - milk, 285, 286
 - starch equivalent, 187
 - fermentation products from, 178
- Crude protein, 4, 200, 201, 211, 214, 242, 247
 - as feeding standard, 200 210, 213
 - components of, 4, 201
 - determination of, 4, 200
 - digestibility of, 150
 - in milk, 267, 272, 273, 289
- Crushing of foods, 150
- Cryptoxanthin, 50, 338
- Crypts of Lieberkuhn, 109
- Curled toe paralysis, 63
- Cyanocobalamin, 71
- Cyanogenetic glycosides, 12, 91, 350
- Cysteine, 36, 39, 82
- Cystine, 36, 209
 - association with methionine, 207, 243, 245
 - in oilseed meals, 345
 - in selenium toxicity, 94
 - in wool, 246
 - sulphur in, 82
- Cytochromes, 85, 98, 99, 125
- Cytosine, 42-44, 138
- Dactylis glomerata* (see cocksfoot)
- Daucus carota* (see carrots)
- Deamination, 118ff, 133, 211, 212
- Dehydroascorbic acid, 74
- 7-Dehydrocholesterol, 32, 33, 54
- Dehydroretinol (see Vitamin A₂)
- Deoxyribonucleic acid (DNA), 42-44
- Deoxyribose, 42
- Dextrins, 7, 17
 - digestion of, 104, 105, 109
- Dhurrin, 12
- Dicoumarol, 60
- Dienoestrol, 363
- Diethylstilboestrol (see stilboestrol)
- Digestible crude protein, 202, 210 214, 228, 231, 289
 - requirements for, growth, 240, 241
 - lactation, 279, 287, 289
 - maintenance, 226-231
- Digestible energy, 158, 163, 182, 190
 - as feeding standard for pigs, 182, 198, 199, 238, 291
- Digestibility, 144ff
 - and intake, 180
 - factors affecting, 149ff
 - in vitro*, 148, 209
 - measurement of, 144ff, 202
 - of grass, 299, 300
 - of hay, 317
 - of proteins, 202
 - of silage, 312
- Digestibility coefficient, 144, 148-151
- Digestive tract, of cow, 107, 114
 - of fowl, 107, 111
 - of pig, 106, 107
- Digestion, 104ff
 - energy loss during, 162
 - in fowls, 111ff
 - in horses, 121, 122
 - in pigs, 106ff

- Digestion, in ruminants, 114ff, 154
 rate of, 154
 work of, 186, 187
- Diglycerides, 109, 112
- Dihydroxyacetone phosphate, 127, 131, 140, 141
- Diiodotyrosine, 35, 37, 90
- Dipeptidases, 105, 106, 109
- Diphosphoglyceric acid, 127, 143
- Diphosphopyridine nucleotide (DPN)
 (*see* nicotinamide adenine dinucleotide)
- Disaccharides, 6, 13, 14
- Distillers' grains, 336
- Diverticulum, 111
- DNA (*see* deoxyribonucleic acid)
- Draff, 335
- Dried grass, 318-321
- Duodenal juice, 108
- Duodenum, 107-109
- Early weaning of pigs, 111
- Echinochloa frumentacea* (*see* millet)
- Effluent (silage), 311
- Egg, 174
 composition of, 258
 shell, 258, 259
 effect of calcium deficiency on, 77
 effect of manganese deficiency on, 92
 yolk, 41
 as source of vitamins, 50ff
- Egg production, 257ff
- Egg white injury, 69
- Eijkmann, 48
- Elastase, 105
- Eleusine coracana* (*see* millet)
- Emden and Myerhof pathway, 126, 140, 142
- Emulsification (during digestion), 109, 112
- Encephalomalacia, 58, 59
- Endergonic reactions, 124
- Endogenous urinary nitrogen (*see* nitrogen)
- Endopeptidases, 105
- Energy, 123ff
 content of body, 234, 235
 content of foods, 156ff, 181ff
 content of liveweight gain, 235, 237
 digestible (*see* digestible energy)
 fixation in plants, 97
 gross (*see* gross energy)
- Energy, measurement of, 157ff, 181ff
 metabolisable (*see* metabolisable energy)
 metabolism, 123ff
 net (*see* net energy)
 productive values for poultry, 198
 requirement for, egg production, 258
 fattening, 231ff
 growth, 157, 174ff, 236ff
 lactation, 274ff, 283, 284, 287, 289, 291
 maintenance, 156, 177, 217ff, 263, 291
 pregnancy, 263ff
 retention, 162, 169, 172
 systems, 181ff
- Enterocrinin, 109
- Enterokinase, 108, 109
- Enzootic ataxia, 87
- Enzymes, 97ff
 action of, 98ff
 denaturation of, 102
 digestive, 104ff
 inhibitors, 101
 in milk, 267
 in plants, 3, 308, 315
 microbial, 115
 nature of, 98ff
 zinc containing, 92
- Ergocalciferol, 33, 53 (*see also* Vitamin D)
- Ergosterol, 33, 54, 297
 absorption of, 114
- Ergot, 341
- Erythromycin, 358
- Escherichia coli*, 60, 66, 362
- Essential amino acid index (EAAI), 208, 209
- Essential amino acids, 35, 38, 137
 importance in protein evaluation, 200ff, 207, 210, 270
 requirements of pigs and poultry, 242ff, 259, 260, 293
- Essential fatty acids, 23, 286
- Esterases, 101, 106
- Esters, 21, 101
- Ether extract, 4, 5
- Haemoglobin, 268
- Exergonic reactions, 124
- Exogenous urinary nitrogen, 227
- Exopeptidases, 105, 106
- Luxative diathesis, 58, 59, 94

- Factorial method of estimating, energy requirements, 274, 291
 mineral requirements, 248, 280
 protein requirements, 228, 229, 239, 240, 278
- Faeces, 110, 144
 collection of, 144, 145, 149, 159
 minerals in, 152, 248
- Fasting, katabolism, 218
 metabolism, 196, 217-222, 263
- Fatal syncope, 58
- Fats, 2, 21ff, 126, 158
 absorption of, 109, 112, 113
 analytical constants of, 24-26
 carotene in, 51
 chemical properties of, 27ff
 composition of, 26, 27
 digestion of, 97, 106, 108, 109, 121
 hydrogenation of, 29, 121
 hydrolysis of, 27
 in liveweight gain, 234-236
 melting point, 24
 metabolism of, 131, 132, 139, 140
 milk, 26, 27, 158, 179, 267ff
 oxidation of, 27, 28, 166
 storage of, 170, 172, 175, 184, 237
 synthesis of, 69, 139-141, 175ff, 270, 282
 taints in, 28, 31
 utilisation of, for maintenance, 173, 174
 for production, 174ff
- Fattening, 175ff, 235
- Fatty acids, 22ff, 59, 110, 131, 266
 absorption of, 109, 112, 121
 efficiency for fattening, 177
 essential, 23, 286
 in milk fat, 27, 179, 269
 oxidation of, 27, 28, 131, 132
 synthesis of, 139, 140
 (see also volatile fatty acids)
- Feather picking, 82
- Feathers, 86
- Feeding standards for, egg production, 257ff
 fattening, 231ff
 growth, 231ff
 lactation, 267ff
 maintenance, 216ff
 pregnancy, 261ff
 reproduction, 252ff
 wool production, 246ff
- Ferric oxide (as marker), 145
- Ferritin, 85
- Fertilisers (nitrogenous), 301
- Festuca ovina* (see sheep's fescue)
- Festuca pratensis* (see meadow fescue)
- Fingerling, 197, 198
- Fischer, 39
- Fish factor, 73
- Fish meal, 91, 242, 352, 353
 as source of, minerals, 78, 79, 81, 91
 vitamin K, 60
- Flavin adenine dinucleotide (FAD), 63, 125ff
- Flavin mononucleotide (FMN), 63, 99, 100, 140
- Flavoproteins, 63, 85, 100
- Flowmeal, 334
- Fluorapatite, 77
- Fluorine, 76, 77, 95, 269
- Flushing, 255
- Flying bent, 298
- Fodder beet, 324-327
 tops, 304
- Foetus, 261
- Folic acid, 67, 68, 260, 270
- Food, digestibility of, 144ff
 energy content of, 156ff
 energy value of, 181ff
 protein evaluation of, 200ff
 unit system, 188, 189
- Forbes, E. B., 183, 275
- Formaldehyde, 307
- Formic acid, 115, 307, 309
- Fowl, absorption in, 112
 digestion in, 107, 111, 112
 liveweight gain in, 235
 utilisation of energy by, 177
 (see also poultry)
- Frap, 198
- Fries, 275
- Fructosans (fructans), 7, 11, 18, 295, 299, 301, 309, 310, 330
- Fructose, 8, 12, 15, 18, 322
- Fructose phosphate, 126, 127
- Fructosides, 12
- Fumaric acid, 128, 133, 134
- Funk, 48
- Furan, 9
- Galactans, 7, 11, 18
- Galactolipids, 11, 21, 31
- Galactose, 6, 11, 12, 15, 18, 19, 31
 in milk, 268
 synthesis of, 142
- Galactosides, 12
- Galacturonic acid, 10, 19
- Gall bladder, 109
- Gallates, 29

- Gallic acid, 29
 Gastric juice, 108, 116
 Gastric mucosa, 105
 Gelatine, 207
 Genistein, 347
 Gizzard, 107, 111
 Gliadins, 41
 Globin, 41
 Globulins, 41
 Glucaric acid, 9
 Glucolipids, 21, 31
 Gluconeogenesis, 175
 Gluconic acid, 9
 Glucosans (glucans), 7, 15ff
 Glucose, 7ff, 31, 158, 166
 as product of digestion, 109
 in glycolipids, 31
 in milk, 268-270
 in pastures, 295
 in pregnancy toxæmia, 266, 267
 metabolism of, 126ff, 141, 162
 utilisation of, for maintenance, 173, 174
 for production, 175, 176
 Glucose-1-phosphate, 10, 142
 Glucose-6-phosphate, 10, 127, 129, 142
 Glucosides, 12
 Glucuronates, 159
 Glucuronic acid, 9, 10, 19, 74
 Glutamic acid, 36, 44, 46, 296, 332
 metabolism of, 133-135, 138
 Glutamic dehydrogenase, 92
 Glutamine, 46, 296
 Glutelins, 41, 337
 Gluten, 337
 Glyceraldehyde-3-phosphate, 126, 127
 Glycerol, 21, 22, 27, 30, 31
 absorption of, 112
 in milk fat, 269
 metabolism of, 131, 135
 production of (during digestion), 109
 synthesis of, 140, 141
 Glycerophosphate, 31, 131, 141
 Glycerose, 7, 35
 Glycine, 35, 36, 44
 in protein synthesis, 136
 requirement by chick, 207, 243, 244, 245
 Glycocholic acid, 109
 Glycogen, 9, 14, 16, 17
 as energy source, 126, 129
 digestion of, 104, 109
 synthesis of, 141
 Glycolipids, 21, 31
 Glycoproteins, 41
 Glycosides, 11, 12, 201
 Goat, requirements of, 287
 Goitre, 90, 265, 304
 Goitrin, 91
 Goitrogens, 90, 91, 304, 346
 Gossypol, 345, 348
 Gramicidin, 358
 Graminan, 18
 Gramineae, 18, 331
 Grass, 295ff
 dried, 318-321
 minerals in, 78ff
 vitamins in, 50ff
 nutritive value of, 297
 (see also pasture)
 Grass factor, 73
 Grinding of foods, 150, 151, 155, 161, 285
 Grit, 78
 Groats, 332, 334
 Gross energy, 157, 158
 fate of, 163
 of milk, 274-276, 291
 Gross protein value (GPV), 203, 210, 211, 345
 Groundout meal, 242, 346
 Groundnuts, 66
 Growth, energy requirements for, 236ff
 energy utilisation for, 178
 feeding standards for, 231ff
 mineral and vitamin requirements for, 247ff
 protein requirements for, 239ff
 Growth stimulating substances, 358ff
 Guanine, 42-44, 138
 Gum arabic, 19
 Gums, 7, 10, 11, 19

 Haem, 41, 99
 Haemoglobin, 41, 84, 86, 248
 Haemosiderin, 85
 Hair, 86, 92, 94
 Halibut liver oil, 50, 54
 Hay, 314ff
 Heat, increment of foods, 161-165, 172, 174, 177, 217, 224
 increment of gestation, 263
 loss from body, 162, 223
 of combustion, 157
 of fermentation, 162, 172, 174, 177
 production, 163ff, 217ff
 Hemicelluloses, 6, 10, 15, 18
 digestion of, 109, 112, 116
 in grass, 295, 299
 in silage, 309

- Hen (see poultry)
 Henneberg, 3
 Herbs, 295, 299
 Heteropolysaccharides, 7, 10, 12, 18
 Hexoestrol, 363, 364
 Hexosans, 7, 15
 Hexose phosphate shunt, 129, 141
 Hexoses, 6, 11, 15, 18
 absorption of, 112
 High energy bonds, 128
 Hippuric acid, 159
 Histamine, 45, 309
 Histidine, 37, 38, 41, 45, 207, 245, 293,
 309, 332
 Histones, 41
 Hofmeister, 39
 Hogg, 88
Holcus lanatus (see Yorkshire fog)
 Holo enzyme, 100
 Holotrichs, 116
 Hopkins, 48
 Hops, 328, 335, 336
Hordeum sativum (see Barley)
 Hormones, 252, 363ff
 adrenal, 32
 insulin, 82
 pituitary, 252
 sex, 32
 thyroxine, 35, 37, 90, 143, 248, 363
 Horse, digestion in, 121, 122
 Hydrochloric acid (in gastric juice), 81,
 108
 Hydrogen cyanide, 12, 350
 Hydrogen sulphide, 110
 Hydrolytic rancidity, 27
 Hydroperoxide, 27
 Hydroxybutyrate, 266, 268, 269
 Hydroxycobalamin, 72
 Hydroxylysine, 35, 37
 Hydroxyproline, 34, 35, 38
 Hydroxyzine, 367
 Hyperketonaemia, 266, 267
 Hypervitaminosis 74
 Hypocalcaemia, 78, 327
 Hypoglycaemia, 266
 Hypomagnesaemia, 83
 Hypomagnesaemic tetany, 80, 83, 84, 113

 Ileum, 107
 Indicators (as markers) 147
 Indole, 110
 Infertility, 52, 256
 Inositol, 73, 270
 Insulin, 82
 International Units, 51, 55, 57
 Intestine, small, 108ff
 large, 109ff
 Intrinsic factor, 70
 Inulin, 7, 18, 330
 Iodinated caein, 363
 Iodine, 76, 90, 91
 absorption of, 114
 deficiency symptoms, 90, 91, 265
 in animal body, 76, 90
 in eggs, 258
 in milk, 269
 reaction with polysaccharides, 16, 17
 requirement for egg production, 259,
 260
 requirement for maintenance and
 growth, 248
 utilisation of, 248
 Iodine Value, 25, 26
 Iron, 76, 84ff
 absorption of, 113
 availability of, 152
 deficiency symptoms, 85
 in animal body, 76, 84, 85
 in eggs, 258
 in grass, 297
 in milk, 270
 in pregnancy, 85, 264
 in proteins, 85, 99
 requirement for egg production, 259
 requirement for maintenance and
 growth 248
 sources of, 85
 taints, 28
 utilisation of, 248
 Isocitric acid, 128
 Isoelectric point, 35
 Isoleucine, 36, 38, 207, 245, 260, 293
 Italian ryegrass, 295, 298

 Jacobine, 47
 Java beans, 12
 Jerusalem artichokes, 330

 Kale, 303, 304, 308
 Kapok, 351
 Katabolism, 123, 156
 Kellner, O., 183-194, 220, 222, 227, 235,
 275, 276
 Keratin, 40, 246
 Ketoglutaric acid, 128, 133 135
 Ketones, 28, 167, 266
 Ketonic rancidity, 28

- Ketoses, 8, 15
 Ketosis, 167
 Kilocalorie, 123, 158ff, 184ff, 219ff, 258ff
 Kjeldahl, 4, 200, 201
 Kuhn, G., 183
- Lactase, 104, 105, 109-111
 Lactation, 267ff
 tetany, 83
 Lacteal, 106, 112
 Lactic acid, 14, 61, 98
 in metabolism, 129
 in rumen, 115, 117
 in silage, 306ff
 Lactic acid bacteria, 115, 308, 309
 Lactic acid dehydrogenase, 98, 129
 Lactoglobulin, 41, 268, 356
 Lactose, 6, 11, 13, 14
 digestion of, 104, 105
 in early weaning, 111
 in milk, 267ff
 synthesis of, 141, 142, 175
 Lamb, carcass composition of, 234
 Lanolin, 30
 Lard, 27
 Large intestine, 109ff
 Laurel oil, 23
 Lauric acid, 22, 23, 26, 30
 Lecithinases, 31
 Lecithins, 21, 30, 31, 70
 Legumes, 295ff
 Legume, hay, 316
 silage, 308
 straw, 323
 Leucine, 36, 38, 207, 245, 260, 293
 Levan, 18
 Level of feeding, 161, 180, 193
 Lignin, 17, 19, 20, 110, 116, 118, 147, 148
 effect on digestibility, 150
 in grass, 296, 299
 Limestone, 78
 Linamarin, 12, 350
 Lind, 48
 Linoleic acid, 22-26, 140, 331
 in milk fat, 268
 in rumen, 121
 Linolenic acid, 22-26, 31, 140
 in milk fat, 268
 in rumen, 121
 Linseed, 12, 24
 cake, 84
 cyanogenetic glycosides in, 12
 meal, 350, 351
 mucilage, 19
 Lipase, 27, 97, 105, 108, 109, 112, 113
- Lipids, 2, 21ff
 classification of, 21
 compound, 21, 30, 31
 digestion of, 121
 in eggs, 258
 in grass, 297
 nitrogenous, 44
 (see also fats)
 Lipolytic hypothesis, 112
 Liver, 3, 113
 copper in, 88, 366
 importance in metabolism, 119, 129, 133
 secretions, 109
 Liveweight gain, 234-236
Lolium multiflorum (see Italian ryegrass)
Lolium perenne (see perennial ryegrass)
 Lotaustralin, 12
 Lucerne, 18, 60, 302-305
 dried, 321
 hay, 316
 Lysine, 37, 41, 45, 106, 296
 as essential amino acid, 38, 207
 available, 208-211
 in cereal grains, 331, 332, 339
 in oilseed meals, 345
 requirement, by chick, 243-245, 260
 by pig, 245, 293
- Magnesium, 76, 77, 83, 84, 302
 absorption of, 113
 availability of, 152, 153
 deficiency symptoms, 83, 84
 in animal body, 76, 83
 in eggs, 258
 in grass, 297-299
 in milk, 269
 losses from body, 248
 sources of, 84
 tetany, 83, 84, 113
 Maintenance, 214ff
 energy requirements for, 156, 217ff
 feeding standards for, 216ff
 mineral and vitamin requirements for, 247-251
 protein requirements for, 226ff
 utilisation of energy for, 172-174
 Maize, by-products, 339, 340
 flaked, 339
 grain, 51, 331, 338, 339
 Malic acid, 128
 Malonyl coenzyme A, 139, 140
 Malt culms, 328, 335
 Maltase, 104, 105, 109-112
 Maltose, 6, 13, 14, 17, 111

- Maltose, digestion of, 104, 105, 109
 Mammary gland, 261, 267-270
 Manganese, 76, 91, 92
 and reproduction, 257
 deficiency symptoms, 91
 in animal body, 76, 91
 in eggs, 258
 in enzyme action, 100
 in grass, 297, 299, 300
 in pastures, 92, 297
 requirements for egg production, 259, 260
 toxicity, 92
 Mangold, root, 324-327
 tops, 304
 Mannans, 7, 11, 18
 Mannose, 6, 11
 Margarine, 29
 Mastitis, 272
 Meadow fescue, 298
 Meat and bone meal, 78, 354
 Meat meal, 354
Medicago sativa (see lucerne)
 Megacalorie, 123
 Melissic acid, 29
 Menadione, 59, 60, 74
 Menaphthone, 59
 Metabolic faecal nitrogen, 149-151, 202, 204, 205, 227ff, 240
 Metabolic liveweight, 219
 Metabolisable energy (ME), 159 165, 172ff, 182ff, 214
 calculation from TDN, 190, 194, 195
 of poultry diets, 223, 238, 239, 244
 requirements for egg production, 258
 utilisation for, fattening, 174ff
 growth, 178, 179
 lactation, 179, 196, 275, 287, 289
 maintenance 172 173, 177, 178, 195 197
 Metabolism, 123ff
 Methaemoglobin, 296
 Methane, 116, 118, 148, 159-161, 167, 170
 Methionine, 36, 82, 94
 as essential amino acid, 38, 207
 association with cystine, 243
 association with glycine, 243
 available, 209, 211
 in cereal grains, 332
 in oilseed meal, 345
 in wool, 246
 requirement by chick, 243-245, 260
 requirement by pig, 293
 Methylmalonyl coenzyme A, 72, 130
 Milk, 267ff
 by products of, 356
 chemical composition of, cow's, 3, 14, 267ff
 ewe's, 267, 269, 289
 goat's, 267, 269, 287
 sow's, 267, 269, 290-294
 fat in, 26, 27, 267ff
 minerals in, 79, 85, 94, 265, 267, 269
 requirements for production of, 267ff
 taunts in, 46, 326
 utilisation of energy for production of, 174, 179, 192, 196
 vitamins in, 50ff, 265
 yields, 271, 283ff
 Milk fever, 77, 283
 Millet, 341
 Minerals, 75ff, 180
 absorption of, 113
 availability of, 152, 248, 249
 deficiency symptoms, 77ff, 257
 essential, 76
 in foods, 297ff, 311, 332
 in grass, 297
 in milk, 265, 267, 269
 losses, 248
 requirements for, egg production, 259
 lactation, 279, 294
 maintenance and growth, 247ff
 toxicity of, 76
 Moisture, determination of, 4
 Molasses, 15, 66, 310, 327, 328
Molma caerulea (see flyling bent)
 Molybdenum, 76, 93, 94
 in enzymes, 93
 in milk, 269
 in pasture, 297, 300
 toxicity of, 87, 93
 Monoglycerides, 112
 Monosaccharides, 6ff, 19, 112
 Morphine, 47
 Morrison, F B, 183
 Mouth (digestion in), 106
 Mucilages, 7, 11, 19, 350
 Mucin, 41, 112
 Mucosal block theory, 86
 Muscle, 125, 174
 Muscular dystrophy, 57-59, 95
 Mycosterols, 32
 Myosin, 125
 Myrcyl alcohol, 29, 30
 Myrcyl palmitate, 30
 Myristic acid, 22, 26
 Myroxanthene, 50

- Naphthoquinones, 59 (*see also* vitamin K)
- Nardus stricta* (*see* white bent)
- Neomycin, 358
- Net energy, 162, 182ff, 193, 194, 197, 300, 301
 determination of, 183ff
 of nutrients, 185
 requirements for, fattening, 191ff
 growth, 236
 lactation, 277
 maintenance, 193, 217ff
 systems for pigs and poultry, 197, 198
 systems for ruminants, 183ff
- Net protein ratio (NPR), 203
- Net protein utilisation (NPU), 206
- Net protein value (NPV), 206
- Neurath, 40
- Nicotinamide, 64, 65, 100
- Nicotinamide adenine dinucleotide (NAD), 64, 100, 124ff
- Nicotinamide adenine dinucleotide phosphate (NADP), 64, 100, 127ff, 175
- Nicotine, 47
- Nicotinic acid, 64, 251, 270
- Niger meal, 351
- Night blindness, 52, 250
- Nitrate reductase, 93
- Nitrates, 44, 46, 296, 301
- Nitrites, 46, 296
- Nitritocobalamine, 72
- Nitrogen, 4, 34, 200ff
 balance, 163, 170, 184, 203-205, 229, 230, 240, 279
 endogenous urinary, 204, 205, 227, 228, 240, 246
 exogenous urinary, 227
 faecal, 145, 143, 149, 204, 226
 metabolic faecal, 149-151, 204, 205, 227-229, 240, 246, 279
 urinary, 145, 161, 166, 168, 204, 226 (*see also* crude protein)
- Nitrogen free extractives, 4, 5
- Non protein nitrogenous compounds, 44ff, 119, 120, 201, 296
- Nucleic acids, 41ff, 137-139
- Nucleoproteins, 41
- Nucleosides, 42
- Nucleotides, 43, 137
- Nutrient requirements (*see* feeding standards)
- Oat, by products, 332, 333
 grain, 331-334
- Oat, straw, 321, 322
- Oat hay poisoning, 46
- Oesophageal groove, 114
- Oesophagus, 107
- Oestrogens, 304, 363
- Oil, 21, 26, 27, 185, 297
 extraction of 343, 344
 (*see also* fat)
- Oilseed cakes and meals, 343ff
- Oleandomycin, 358, 360
- Oleic acid, 22, 26, 29, 30, 331
 in milk fat, 268
 synthesis of, 140
- Oligo-1,6-glucosidase, 104, 105, 109
- Oligosaccharides, 7, 12, 15
- Oligotrichs, 116
- Olive meal, 351
- Omasum, 107, 114, 116, 117
- Onobrychis sativa* (*see* sainfoin)
- Ornithine, 134
- Orotic acid, 73
- Oryza sativa* (*see* rice)
- Osteomalacia, 55, 77, 79
- Ova, 254-256
- Overfeeding, 255, 256, 265
- Overheating, of hay, 318
- Oxalacetic acid, 98, 128-135
- Oxalic acid, 113, 304
- Oxalsuccinic acid, 128
- Oxidation, 124ff, 157, 166, 315
- Oxidative decarboxylation, 126
- Oxygen, 165ff
- Oxytetracycline, 358-361
- Palatability, 241
- Palmitic acid, 22, 26, 30, 269
- Palmitoleic acid, 22
- Palmito-oleo-stearin, 23
- Palm kernel meal, 349
- Pancreas, 105, 108
- Pancreatic juice, 108, 109
- Panicum nileaceum* (*see* millet)
- Pangamic acid, 73
- Pantothenic acid, 66, 260, 265, 270
- Para amino benzoic acid, 68, 102
- Parakeratosis, 93
- Parathyroid glands, 77
- Parotid glands, 106
- Parasit, 328
- Partition theory, 112
- Pastinaca sativa* (*see* parsnip)
- Pasture, 295 f
 in minerals, 78 f
 (*see also* grain)
- Pear, 61, 64, 303

- Peat scours, 87
 Pectase, 19
 Pectic acid, 19
 Pectic substances, 7, 19
 Pectin, 19, 302
 Pectinic acid, 19
 Pelleting of foods, 161
 Penicillin, 118, 358-361
Pennisetum typhoideum (see millet)
 Pentamethylene diamine, 309
 Pentanone, 28
 Pentosans, 10, 15
 Pentoses, 6, 10, 15, 18, 41, 42, 112, 309
 Pepsin, 104-110, 116, 202
 Pepsinogen, 108
 Peptide linkage, 39, 138, 162
 Peptides, 39, 105, 139
 Perennial ryegrass, 298
 Perosis, 70, 92
 Phaeophytin, 309
 Phenol, 29, 110
 Phenylalanine, 37, 45, 106, 138, 293, 309
 as essential amino acid, 38, 207
 association with tyrosine, 243, 245
 Phenylethylamine, 45, 309
 Phleain, 18
 Phlein, 7, 18
Phleum pratense (see Timothy)
 Phosphocreatine, 125, 126
 Phosphoenolpyruvic acid, 124, 127ff
 Phosphoglyceric acid, 127, 136
 Phospholipids, 21, 30, 70, 268
 Phosphoproteins, 41
 Phosphopyruvic acid, 136
 Phosphoric acid, in lipids, 21, 30, 31
 in metabolism, 124ff
 in nucleic acids, 42, 43
 in proteins, 41, 42
 Phosphorus, 76, 70-80
 absorption of, 113
 association with carbohydrates, 10, 16, 78
 availability of, 79, 152, 153
 deficiency of, 79, 180
 for reproduction, 257
 in eggs, 258
 in grass, 297-301
 in metabolism, 124ff
 in milk, 267, 269, 279, 287, 289
 interrelation with, calcium, 78
 magnesium, 83
 manganese, 92
 vitamin D, 55
 zinc, 93
 Phosphorus, requirements for, egg production, 259, 260
 lactation, 280, 281, 287ff
 maintenance and growth, 249
 Phosphorylation, 112, 124ff
 Phosphoserine, 136
 Phosvitin, 41
 Phytase, 80
 Phytates, 79, 80, 113, 153, 259, 332
 Phytic acid, 79, 113
 Phytosterols, 32, 114
 Pica, 79
 Pig, composition of, 233, 234
 critical temperature of, 224
 digestion and absorption in, 106ff, 151
 energy, requirements for, 223, 237, 238, 291
 systems for, 182, 197, 198
 utilisation by, 176, 177
 feeding standards for, growth, 231ff
 lactation, 290
 maintenance, 216ff
 reproduction, 253ff
 growth of, 232
 growth stimulating substances for, 359ff
 liveweight gain, 235
 mineral deficiencies in, 77ff
 mineral requirements for, 248
 protein evaluation for, 200ff
 protein requirements for, 242ff, 293
 vitamin deficiencies in, 53ff, 256
 vitamin requirements for, 251
 Piglet, anaemia, 85
 digestion in, 110
 Pigments (in milk), 268
 Pining, 88, 89
 Pituitary hormones, 252
Plantago spp (see plantain)
 Plantain, 299
 Poan, 18
 Polenske Value, 26
 Polyneuritis, 62
 Polynucleotides, 43
 Polypeptides, 39
 Polysaccharides, 7, 12, 15ff, 295
 digestion of, 108, 112, 115, 118
 microbial, 117
 Postabsorptive state, 218
 Potassium, 76, 80, 81
 in eggs, 258
 in grass, 297
 in milk, 269
 interrelationship with magnesium, 80

- Potassium, losses from body, 248
- Potato, 16, 328, 329, 330
silage, 308, 312
- Poterium sanguisorba* (see burnet)
- Poultry, amino acid requirements for, 245, 260
digestibility measurements with, 145
digestion in, 107, 111, 112
energy, requirements for, 223, 238, 239, 258
systems for, 182, 198, 199
feeding standards for egg production, 257ff
growth stimulating substances for, 360
mineral deficiencies in, 77ff
requirements for, 259
protein requirements for, 203, 209, 210, 242ff
vitamin deficiencies in, 53ff, 256
requirements for, 251
(see also fowl)
- Pregnancy, 261ff
anabolism, 263
toxæmia, 266, 267
- Procarboxypeptidase, 108, 109
- Productive energy, 198, 239
- Progestogens, 363
- Proline, 34, 38, 44
- Propionic acid, 110, 115, 117
as energy source, 129-131, 135
efficiency of utilisation, for maintenance, 173
for production, 175, 176, 179
in silage, 309
- Propionyl coenzyme A, 130
- Prosecretin, 108
- Protamins, 41
- Proteases, 105
- Protein concentrates, 343ff
- Protein efficiency ratio (PER), 202, 345
- Protein equivalent (PE), 211, 240
- Protein replacement value (PRV), 203, 204
- Proteins, 3, 34ff, 185, 214
absorption of, 113
available, 229
classification of, 40
derived, 43
digestibility of, 202, 210
digestion of, 105ff, 118ff
evaluation of, 200ff
in carcass, 234, 235
in eggs, 258
in grass, 296
in liveweight gain, 235, 236
- Proteins, in milk, 268
metabolic faecal, 229
microbial, 119, 120, 211, 212
oxidation of, 166, 167
properties of, 40
requirements of, for egg production, 259
for growth, 239ff
for lactation, 275, 278, 279, 283, 284, 293
for maintenance, 226ff
for reproduction, 256, 264
for wool production, 246, 247
storage of, 170, 184
structure of, 38
synthesis of, 119, 135ff, 175, 178, 204
utilisation of, for maintenance, 173, 174
for production, 176
- Proteolytic enzymes, 105, 112
- Protopectin, 19
- Protopectinase, 19
- Protozoa, 116, 117
- Proventriculus, 107, 111
- Provitamins, 49, 50, 54
- Proximate analysis of foods, 3-5
- Pseudoglobulin, 268
- Pteridium aquilina*, 62
- Pteroylmonoglutamic acid, 67, 68
- Pyalin, 108
- Purine, 42, 44
- Putrescine, 45
- Pyran, 8
- Pyridoxal, 65
- Pyridoxamine, 65
- Pyridoxine, 65
- Pyrimidine, 42, 44
- Pyrophosphate, 125ff
- Pyruvic acid, 61, 98, 124ff
- Quinine, 47
- Quinones, 29
- Radioactive isotopes, 76, 152
- Raffinose, 6, 14, 15, 295
- Rancidity, 27, 28
- Rape, 303
- Rauwolfia, 367
- Rectum, 107
- Red clover, 299
- Reichert-Meißl Value, 26
- Rennet, 357

- Rennin, 104-106
 Reproduction, 252ff
 Reserpine, 367
 Respiration chamber, 163, 167-170
 Respiratory exchange, 165-169
 Respiratory quotient, 166, 167, 218
 Reticulum, 107, 114, 117
 Retinol (*see* vitamin A)
 Rhamnose, 19
 Rhodopsin, 52
 Riboflavin, 62, 63, 270
 requirements for, 251, 260, 265
 Ribonucleic acid (RNA) 10, 42, 43, 137ff
 Ribose, 10, 11, 42, 62, 124
 Ribosomes, 137
 Rice, 331, 340
 Ricinine, 47
 Rickets, 48, 55, 77, 79, 260
 Roots, 324ff
 Roy, J H B, 240
 Rumen, digestion in, 107, 114ff, 154, 174
 protein breakdown in, 119, 211, 212
 synthesis of vitamins in, 61, 72, 89
 Ruminants, antibiotics in the diet of, 360
 digestibility measurements with, 144,
 150, 151, 152
 digestion in, 107, 114ff
 energy requirements for, 217ff, 261ff
 energy systems for, 182, 183ff
 growth stimulating substances for,
 360, 361
 protein evaluation for, 211-213
 protein requirements of, 228ff, 278ff
 Rye, grain, 340, 341
 straw, 323
 Ryegrass, 18, 300, 301

 Saccharic acid (*see* glucaric acid)
 Sainfoin, 302
 Saliva, 105 108, 114, 119, 212
 Salivary glands, 106
 Salt (*see* sodium chloride)
 Salt peptisability, 212
 Saponification value, 25, 26
 Scandinavian food unit system, 188
 Scleroproteins, 41
 Scurvy, 48
 Seaweed, 14, 91
 Sebaceous glands, 246
Secale cereale (*see* rye)
 Secretin, 108
 Selenium, 76, 94, 95, 269
 interrelation with vitamin E, 58, 59
 toxicity, 94, 350

 Serine, 31, 36, 41, 44, 136
 Sesame, 351
Setaria italica (*see* millet)
 Sheep, digestibility trials with, 145, 146,
 151, 152
 digestion by, 114ff
 energy, requirements of, 217ff, 264,
 265, 289
 utilisation by, 173, 176
 feeding standards for, growth, 231ff
 lactation, 287ff
 maintenance, 216ff
 reproduction, 253ff
 flushing of, 255
 liveweight gain, 234-237
 mineral requirements of, 247-249, 289
 protein requirements of, 226ff, 239ff,
 264, 289
 vitamin requirements of, 250
 Sheep's fescue, 298
 Siderophilin, 85
 Silage, 306ff
 Silicon, 269
 Skatole, 110
 Skim milk, 356
 Small intestine, 105, 108, 109, 117, 119
 Soap, 25, 27
 Sodium, 76, 80, 81, 259
 in eggs, 258
 in milk, 269
 losses from body, 248
 Sodium chloride, 81, 82, 282, 287
 iodised, 91
 requirements, 259, 281, 282
 toxicity, 82, 259
 Sodium metabisulphite, 306, 307
 Solanine, 47, 328, 329
Solanum tuberosum (*see* potato)
 Solids-not-fat, 267-273, 283, 289
 Sorghum, 341
 Soya bean meal, 346
 Specific dynamic effect, 162
 Spermaceti, 30
 Spermatozoa, 254-256
 Sphagnum moss, 328
 Sphingomyelins, 21, 30, 31
 Sphingosine, 31
 Stachyose, 6, 15, 295
 Stage of growth (of plants), 299, 310,
 317
 Starch, 9, 14-17, 104, 158, 299, 302
 digestion of, by fowls, 111
 by pigs, 108, 109
 by ruminants, 114ff, 120
 in cereal grains, 332

- Starch, in determination of starch
 equivalent, 184, 185, 188
 in potatoes, 328
 utilisation for, maintenance, 173
 production, 176
- Starch equivalent, 16, 183ff, 197, 214
 calorific values of, 191, 192
 determination of, 183ff, 194
 of legumes, 303
 requirements for, fattening and
 growth, 192, 236
 maintenance, 191-193, 220-223
 milk production, 192, 276-278, 287,
 289
- Steaming up, 264
- Stearic acid, 22, 26, 29, 30, 121
- Sterility, 256
- Steroisomers, 8, 9
- Sterols, 32, 33, 49, 54
- Stilboestrol, 363, 365
- Stohmann, 3
- Stomach, 107, 108, 114
- Straw, 57, 321ff
- Streptococci, 209
- Streptococcus lactis*, 14
- Streptomycin, 358, 361
- Strontium, 76, 95, 96
- Strychnine, 47
- Sublingual glands, 108
- Submaxillary glands, 108
- Substrate, 101
- Succinic acid, 115, 117, 127, 128
- Succus entericus, 108, 109
- Succinyl coenzyme A, 72, 127, 128, 130
- Sucrose, 14, 104, 105, 109-112
- Sucrose, 6, 11-15, 18, 111, 295, 299
 digestion of, 104, 105
 in roots, 324ff
- Sudoriferous glands, 246
- Sugar beet, 14, 45, 324-327
 molasses, 327
 pulp, 327
 tops, 304, 308
- Sugars, 7ff
 digestion of, 104ff, 116
 in grass, 295ff
 in roots, 326, 327
 in silage, 308-310
- Suint, 246
- Sulphanilamide, 102
- Sulphonamides, 101
- Sulphur, 34, 76, 82, 258
- Sulphur dioxide, 307
- Sunflower meal, 64, 351
- Surface area (of animals), 218
- Surfactants, 367
- Swayback, 87, 265
- Swede, root, 325, 326
 tops, 303, 304
- Sweet clover disease, 60
- Taints, 28, 31, 46, 353
 in milk, 46, 326
- Tallow, 27
- Taurocholic acid, 109
- Teart, 87, 93, 300
- Temperature, body, 2, 223-225
 critical, 224, 225
 silage, 308
- Tetany, 80, 83, 113
- Tetracyclines, 358-362
- Tetrahydrofolic acid, 136
- Tetrahymena, 209
- Tetrasaccharides, 6, 15
- Thermal equivalent, 166, 167
- Therm, 183
- Thiaminase, 62
- Thiamine, 49, 61ff, 82, 250, 270
- Thiocyanate, 91
- Threonine, 36, 38, 41, 207, 245, 260, 293
- Thymine, 42, 44
- Thyroglobulin, 90
- Thyroid gland, 90
- Thyroproteins, 363
- Thyroxine, 35, 37, 90, 143, 248, 363
- Timothy, 18, 298-300
- Tin, 269
- Tocopherols, 29, 56
 (see also vitamin E)
- Total digestible nutrients (TDN), 151,
 152, 183, 189, 190, 194, 195, 198,
 214
- Trace elements, 84ff
- Tranquillisers, 366
- Transamination, 38, 46, 133, 135
- Transmethylation, 70
- Trefoil, 18
- Trehalase, 104, 105, 109
- Trehalose, 6, 13, 14, 104, 105
- Tricarboxylic acid cycle, 127ff, 266
- Tributyrin, 25
- Trifolium pratense* (see red clover)
- Trifolium repens* (see white clover)
- Triglyceride, 22, 23
- Trimethylamine, 31, 46
- Trolein, 23
- Tripalmitin, 25, 166
- Triphospho-pyridine nucleotide (TPN)
 (see nicotinamide-adenine di-
 nucleotide phosphate)

- Trisaccharides 6 14 15
Triticum aestivum (see wheat)
 True protein, 119, 201
 Trypsin, 105-109
 inhibitor, 346
 Trypsinogen, 108
 Tryptamine, 45, 309
 Tryptophan, 38, 45, 64, 65, 138, 207,
 245, 260, 293, 309
 in cereal grains, 332, 339
 Tubers, 324, 328ff
 Turacin, 86
 Turkeys, 243, 360
 Turnip, roots, 3, 57, 324-326
 tops, 303, 304
 Twin lamb disease, 266
 Tyramine, 45
 Tyrosine, 37, 45, 90, 106, 207, 243, 245,
 260
 Tyrothricin, 358

 Ubiquinone, 57
 Ultra-violet light, 54, 63
 Underfeeding, 255, 264, 283
 Uracil, 42, 138
 Urea, 46, 82, 98, 101, 119 121, 212, 323
 in milk, 267, 268
 in saliva, 119
 metabolism of, 134, 136, 226
 Urease, 98, 101
 Uric acid, 145
 Uridine phosphate, 142
 Urine, 119, 145, 212
 energy loss in, 159-161, 166
 minerals in, 80, 81, 248
 Uronic acids, 9, 10, 18, 19

 Valeric acid, 117
 Valine, 36, 38, 138, 207, 245, 260, 293
 Value numbers, 187
 Vetches, 303
 Vicianin, 12
 Villi, 106, 109, 112
 Vinkush, 88
 Virtanen, A. I., 307
 Vitamin A, 50ff, 265, 270, 297
 absorption of, 114
 chemical nature of, 50
 hypervitaminosis, 74
 metabolism of, 52
 requirements for, egg production, 260
 growth, 250
 lactation, 282
 symptoms of deficiency, 52, 256, 264,
 265
 Vitamin A₂, 50
 Vitamin B₁ (see Thiamine)
 Vitamin B₂ (see Riboflavin)
 Vitamin B complex, 60ff, 243, 267, 270,
 282, 283, 297
 requirements for, egg production, 260
 growth, 251
 synthesis of, in intestine, 121
 in rumen, 115, 121
 Vitamin B₆, 65, 270
 Vitamin B₁₂, 70-73, 88, 89, 121, 260, 270
 in antibiotic residues, 358
 Vitamin C, 73, 74, 114, 267, 270, 319
 Vitamin D, 32, 33, 53ff, 77, 265, 270, 297
 absorption of, 114, 153
 and radiant energy, 54
 chemical nature of, 53
 hypervitaminosis, 74
 in roughages, 316, 320
 metabolism of, 55
 potency of different forms, 56, 261
 requirements of, for egg production,
 260
 for lactation, 283
 symptoms of deficiency, 55
 Vitamin E, 56ff, 265, 270
 absorption of, 114
 chemical nature of, 56
 in grass, 297
 interrelations with selenium, 94
 metabolism of, 57
 symptoms of deficiency, 57, 256
 Vitamin K, 59ff, 270
 absorption of, 114
 chemical nature of, 59
 hypervitaminosis, 74
 metabolism of, 60
 symptoms of deficiency, 60
 synthesis of, 60, 121
 Vitamins, 3, 48ff
 absorption of, 114
 and energy utilisation, 180
 availability of, 251
 in cereals, 332
 in dried grass, 319, 320
 in milk, 270
 requirements of, for egg production,
 260
 for lactation, 282, 294
 for maintenance and growth, 250,
 251
 synthesis of, 61ff, 211
 Volatile fatty acids, 110
 absorption of, 112
 in rumen, 117, 188, 275, 286

- Volatile fatty acids, metabolism of, 125, 129-132, 139, 140
 utilisation of, for maintenance, 173, 174
 for production, 175-178
- Water, 1, 2, 258, 267
 in animal body, 1, 234-236
 in foods, 2
 in salt poisoning, 82
 metabolic, 2
- Waxes, 21, 29, 30, 246
- Whale meal, 354
- Whale solubles, 353
- Wheat, grain, 331, 336ff
 by products, 337, 338
 straw, 323
- Whey, 357
- Whey factor, 73
- White bent, 298
- White clover, 299
- White fish meal, 345, 352
- Wood, T. B., 188, 193, 222, 223
- Woodman, 277, 284
- Wool, 82, 174
 minerals in, 82, 86, 92
 pigmentation of, 86
- Wool, production of, 246, 247
- Xanthine oxidase, 93
- Xerophthalmia, 52, 53
- Xylans, 7, 15
- Xylose, 10, 11, 15, 18
- Yarrow, 299
- Yeast, brewers', 335, 336
 vitamins in, 61ff
- Yorkshire fog, 298
- Zea mays* (see maize)
- Zein, 339
- Zinc, 76, 92, 93
 absorption of, 114
 deficiency symptoms, 92
 in animal body, 76
 in grass, 297
 in milk, 269
 requirement of, for egg production, 259, 260
 toxicity of, 93
- Zoosterols, 32
- Zwitter ions, 35
- Zymogens, 104

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